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Phenology and Branching

in

eight selected species

of

the genus *Cliffortia*

by

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Since the creation of the world God's invisible qualities - his eternal power and divine nature - have been clearly seen, being understood from what has been made, so that men are without excuse. The Holy Bible, Romans 1: 20.

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Phenology and Branching in eight selected species of the genus *Cliffortia*

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Chapter 1: INTRODUCTION

Abstract:

To date the peculiarities of the inflorescence structure in the wind-pollinated genus *Cliffortia* (Rosaceae), has gone unnoticed. In this study stereo microscope examination and sketching of fresh and dried specimens, combined with extensive field observations, were performed on eight species of the genus.

In its simplest form the inflorescence is a reduced short shoot, bearing a lateral e-bracteate flower and a potentially viable apical bud. Variations in the basic structure can be in the number of flowers, the mix of the sexes of the flowers and the number and type of short shoots as primary, secondary and tertiary axes. A high incidence of structural plasticity of the inflorescence exists. Structural changes can take place throughout the development of the inflorescence or only at the onset of the vegetative stage. These changes occur in the short shoot(s) constituting the axes of the inflorescence, causing either an increase in the length of the internodes, apical proliferation of the axes or a combination of these two effects. A specific combination of changes is linked to a specific inflorescence type. The vegetative elements of the inflorescence thus modified, are retained as an integral part of the vegetative branching system, instead of being discarded after the shedding of the fruits. Thus the inflorescence disappears without being discarded, while the integration of the inflorescence matrix into the vegetative elements of the plant, has a marked effect on the vegetative branching pattern.

In some species the structural changes in the inflorescence are linked to changes in the predominance of one sex over the other over time, so that an individual, initially of the one sex, can become one of the opposite sex by the end of the season. In the past the erroneous interpretation of a single point in the process of a sex change as if it is a permanent state of sexuality, led to the prevalent acceptance of dioecy as the norm for the genus, while in truth, it is monoecy with dichogamy in this genus, as in many other wind-pollinated taxa.

Key words: *Cliffortia,* inflorescence, branching, dioecy, monoecy, dichogamy, sex change, morphological plasticity.

The genus *Cliffortia,* consisting of evergreen plants of widely varying growth forms, belongs to the family Rosaceae, section Sanguisorbeae, group apetalae (Weimarck 1934) and is closely related to the genera *Acaena, Sanguisorba* and *Alchemilla.* Eriksson et al. (1998) found the elements of the section Sanguisorbae to have strong links with each other and to be not simply an artifact of convergent evolution. The entire section including *Cliffortia* is wind-pollinated and has, therefore, unisexual and unobtrusive flowers with stigmas and stamens as their most prominent parts; the flowers often variously aggregated.

Two genera, totally unrelated to *Cliffortia,* viz. *Aspalathus* (Fabaceae) and *Anthospermum* (Rubiaceae), exhibit morphological convergence in vegetative parts, to *Cliffortia.* Nineteen species of *Aspalathus* are indistinguishable in the sterile state from as many species of *Cliffortia*, except for the absence of leaf sheaths and stipules (Dahlgren 1971). At the same time an amazing diversity of leaf form exists within the relevant species of each genus. Several species of *Anthospermum,* sharing habitats with *Cliffortia* species, are indistinguishable from these species. The similarity extends beyond the presence of leaf sheaths and stipules to include flower morphology, both having small unisexual flowers, prominent calyx lobes and remarkably similar fruits.

Cliffortia contains 119 species, occurring mainly in the southernmost parts of southern Africa with some spreading northwards up the subtropical eastern coastal areas, while two are limited to the tropical region of central Africa. The majority of the southern African species are endemic to the fynbos vegetation of the Cape Floral Kingdom. Although a very prominent element in the fynbos, *Cliffortia* is the only representative of the Rosaceae in that biome. To date it has been a widely held view that the majority of species are dioecious.

Literature on the Rosoideae (Rosaceae) reflects scant attention to the genus *Cliffortia*. Neither Kalkman (1988) or Eriksson (1998) refers to *Cliffortia,* though Kalkman describes the inflorescence in the Rosaceae as 'varied...most often in racemes.....with or without a terminal flower....or thyrsi with all axes provided with a terminal flower'. He concludes that 'comprehensive research into the structure of inflorescences might reveal evolutionary lines which are now untraceable'. Nordborg (1966) mentions *Cliffortia* only in passing as an African representative of the tribe Sanguisorbae.

The most recent revision of the genus was by Weimarck in 1934. This was preceded by his publication in 1933 of the description of a new species, and followed by the recording of new species in 1940 and 1946. His taxonomic survey of the genus was published in 1948, followed in 1953 and 1959 by the recording of more new species. In all his writings his approach was purely morphological. His infra-generic classification was based on the number of styles present and the distinction between species on leaf and receptacle morphology. Compound inflorescences were not examined in detail. His conclusions as to the presence or absence of short shoots in a particular species, rested on superficial observations made at a single encounter.

Additional new species were published by Oliver and Fellingham (1991, 1994) and by Fellingham (1995). Further notes on single species were published by Fellingham (1993a, 1993b, 1994).

To date the inflorescence has received scant attention. Weimarck (1934) stated that in 'the majority of the representatives of the genus the flowers are borne solitary in the axils of ordinary, vegetative leaves'. As exceptions with more complex inflorescences, he named *C. arborea* Marloth and *C. odorata* L.f. In *C. arborea* he recognized a species possessing several unique morphological characters and described the flowers as 'closely clustered in groups of 5-8 in the axils of simple leaves on very contracted twigs'. These he noted, were bunched together in such a way as to give the impression of a 'spadix'. While clearly pointing to the elongated compact cones found on herbarium sheets containing fertile material, it over simplifies the true situation. In *C. odorata* the flowers occur in contracted racemes of 5 - 15 flowers, which he noted 'approach the form of heads'. He also noted that in this species male and female flowers are frequently found in the same inflorescence. However, in a later review of the genus (Weimarck 1948) he placed this species in a division of the key which described the flowers as 'at least the male, fascicled in the leaf axils', leaving uncertainty concerning the female flowers. In the large-leaved, large-flowered *C. crenata* L.f., Weimarck did notice that the male flowers can occur singly or in pairs or three together in a leaf axil, but the female flower was treated as being 'solitary in the axil of an ordinary vegetative leaf'. In his original description of *C. heterophylla* (1933), he failed to recognize the terminal tubular structure of imbricate modified leaves for which he named the species, as the female inflorescence. The fact that this publication also lacks a description of the flowers, may indicate that he missed the importance of the tubular apical structure as being the female inflorescence altogether. In describing the leaves in *C. ruscifolia*, Weimarck mentioned that the apex can be simple or tri-dentate and linked the variation in hairiness to age. He failed to recognize the simple leaf as the vegetative and the tri-dentate as the bract or subtending leaf and thereby failed to recognize the compact inflorescence.

Studies of the inflorescence in particular, did not include the genus *Cliffortia*. Briggs and Johnson (1979), while making Troll's (1964, 1967) 'Die Infloreszenzen' more accessible to the non-German reader, deals exclusively with the Myrtaceae. Similarly, Weberling (1983, 1989) in his work on inflorescence morphology, makes no mention of the condition in *Cliffortia* or the

Rosaceae for that matter.

My interest in the inflorescence in *Cliffortia*, was kindled by the discovery of highly specialized female inflorescences in *C. conifera* and *C. arborea* (Oliver & Fellingham 1994) and soon after, yet another species in the section *Arboreae,* viz. *C. dichotoma* MS. These inflorescences are cone-shaped with three orders of highly condensed axes. A second and equally remarkable character shared by these species is that of monoecy, with the small clusters of male flowers borne on the same branches as the female cones. A third phenomenon that became apparent in these species is the link between the inflorescence type and the vegetative branching pattern, that develops during the subsequent vegetative phase.

These findings established the existence of a wide range of inflorescence types in *Cliffortia*, varying from solitary flowers to fascicled flowers and highly condensed cones containing large numbers of flowers, but at the same time raising some questions: Is there a common basic construction discernable in all the inflorescence types, how can this account for the apparent dioecy in the genus and, how does the inflorescence type influence the branching pattern?

In order to interpret the inflorescence structure, an understanding of the occurrence, development and function of short shoots in relation to long shoots, is necessary. Questions concerning the connection between the fertile stage and short shoot development and the vegetative stage and long shoot development, have to be addressed. The same holds for the relationship between the sexuality of the flower and its flower-bearing shoot: can flowers be borne on long shoots or perhaps the male flowers only? What happens to the inflorescence matrix at the end of flowering, particularly in species with the inflorescence terminally on the main stem? An important factor in the interpretation of the inflorescence structure is the stance of the individual flower: does the pedicel originate directly in the axil of the subtending leaf or laterally on a highly condensed short shoot inflorescence in the axil of the subtending leaf? Furthermore, the view that the majority of species are dioecious needs testing and the branching patterns studied.

As used in this paper, a short shoot is defined by its short internodes. It is not, however, always a permanent element of the plant morphology but can disappear through abortion, or transformation into a long shoot. It is also not always a patently visible structure but can be completely and permanently hidden in the axil of its subtending leaf. The matrix for the flower-bearing short shoots is provided by the long shoot, which is a vegetative shoot with long internodes. Ordinary vegetative leaves on the long shoots subtend these fertile short shoots. The main involvement of the short shoot is with flower-bearing, with the flowers either bracteate or e-bracteate but never subtended by ordinary vegetative leaves. Vegetative short shoots do occur, but only rarely and then they bear ordinary vegetative leaves, as long shoots do. A short shoot is thus a permanent or temporary, patent or obscure shoot with short internodes, has the main function of flower-bearing and occurs in the axil of a vegetative leaf on a long shoot, or rarely on a vegetative short shoot.

Concerning plant sexuality, Weimarck (1934) noted that 'the distribution of male and female flowers has been shown to be very irregular so that, as far as is known, not less than 47 species out of 78 have been found at least capable of being monoecious'. None the less, he still held the notion of dioecy as the rule for the genus. Evidence gathered during the present study, shed new light on the question of sexuality.

Weimarck (1934) mentioned the branching pattern in connection with the flowering phase by stating that 'if brachyblasts are produced then the flowers are always situated on them, often one flower in the axil of each leaf', adding elsewhere that 'when only elongated branches are formed the stem and branches are, as a rule, sparsely ramified'. Indeed, in *C. crenata* the lax sparsely branched appearance of the plant seems to support his view that all the species in the section Bifoliolae (which includes *C. crenata*) as well as the single-leaved *C. odorata,* have 'elongated branches alone'. However, he failed to observe any relationship between inflorescence type and branching pattern.

Chapter 2: METHODS and MATERIAL

Field observations were done on the plant communities, taking note of seasonal and climatic changes and other stress factors like the constriction caused by a twiner or the removal of main inflorescences as encountered in the study of *C. heterophylla*. Where possible collections of fresh material were made repeatedly from the same populations, over a season or more.

Fresh and dried specimens were dissected, examined and sketched with the aid of a stereo microscope fitted with a camera lucida. The dried material was softened by boiling and soaking in diluted dishwashing solution before dissection. The majority of drawings were done using the camera lucida. The larger fresh specimens were drawn free hand. Mounted specimens were examined under the stereo microscope or by eye.

The choice of species for this study was based on their diversity of inflorescence structure. The most specialized are the three cone-bearing species, *C. conifera*, *C. dichotoma* and *C. arborea*. A highly condensed inflorescence, though with an amazing plasticity, is found in *C. odorata* which also appears to have no short shoots. In *C. heterophylla* the inflorescence is clearly demarcated and initially condensed but extremely plastic and impermanent. The multi-flowered form of the short shoot inflorescence with bracteate flowers, is represented by *C. ruscifolia*. The apparent lack of short shoots (and flowers) in *C. crenata*, makes it an interesting and important subject. *C. nivenioides* is an exceptional and therefore very interesting species for two reasons. It has a preponderance of short shoots, the majority of which are vegetative and the rarer fertile ones appear to bear single flowers directly in the axils of ordinary vegetative leaves.

The following species were studied:

1. C. nivenioides Fellingham

In the process of describing this new species, field work in and around the type locality, north of Blesberg in the Swartberg Mountains, was followed by detailed examination of fresh and herbarium material. The fresh material was from the collections *Fellingham & Vlok* 1588. (K, MO, NBG, PRE) and *Viviers & Vlok* 470 (BM, BOL, K, MO, NBG, P, PRE, S), the latter being also the voucher for the illustrations by Inge Oliver.

Herbarium specimens examined:

Bond 1754 (NBG, PRE); *Thompson* 2275 (NBG, PRE); *Vlok* 1326 (NBG, PRE).

2. C. crenata L. f.

Field work on this species was done in the Anysberg. The fresh specimen, *Oliver* 10387(NBG) was examined in the herbarium and sketched.

Herbarium specimens examined:

Acocks 19280 (NBG); *Barker* 8263 (NBG); *Bean & Trinder-Smith* 2733 (BOL); *Bolus* 2754 (NBG), 7600 (BOL, NBG); *Bond, W* 1511 (BOL); *Boucher 4193* (NBG), 5019 (NBG); *Compton* 3040 (BOL), 3459 (BOL), 3920 (BOL), 5685 (NBG), 7412 (NBG), 8662 (NBG),10830 (NBG),11831 (NBG),18425 (NBG), 18523 (NBG), 22216 (NBG), 22247 (NBG), 22843 (NBG); *Esterhuysen* 3447 (BOL), 5139 (BOL), 5241a (NBG), 5263a (BOL), 10346 (BOL), 13959 (BOL), 25911 (BOL), 27596 (BOL); *Fellingham* 1533 (NBG); *Gillett* 1908 (BOL, NBG); *Goldblatt* 2162 (NBG); *Hugo* 911 (NBG); *Hutchinson* 1123 (BOL); *Kruger* 1204 (NBG, PRE), 1346 (NBG, PRE); *Levyns* 2051 (BOL), 2460 (BOL), 6167 (BOL), 6444 (BOL), 6511 (BOL), 8010 (BOL), 8975 (BOL), 9210 (BOL), 11194 (BOL); *Lewis* 6065 (NBG); *Marloth* 1977 (NBG), 9089 (BOL); *Mauve* et al. 28 (NBG); *McDonald* 1688 (NBG), 1732 (NBG); *McOwan* STE-U13375 (NBG); *Oliver* 4252 (NBG); *Olivier* sn. (NBG); *Pillans* sn. (BOL); *Rehmann* 2716 (BOL); *Salter* 6335 (BOL); *Schoncken* 269 (NBG); *Simpson* 93 (NBG); *Taylor* 4728 (NBG), 8023 (NBG), 9517 (NBG); *Thode* 4818 (NBG); *Tyson* 766 (BOL, NBG); *Van Niekerk* 763 (BOL); *Van Wyk* 536 (NBG);*Van Zyl* 3363 (NBG); *Walters* 1741 (NBG); *Wurts* 1366 (BOL, NBG).

3. C. ruscifolia L.

Fresh specimens examined and sketched were *Oliver* 10567 (NBG), 10569 (NBG) & 10574 (NBG), all from the Touwsberg area.

Herbarium specimens examined:

Barker 5593 (BOL); *Barnes* sn. (BOL); *Bolus* 10603 (BOL), 12674 (BOL); *Boucher* 502 (NBG, PRE); *Burman* 895 (BOL); *Compton* 3039 (BOL), 9492 (BOL); *Durand* 263 (NBG, PRE); *Esterhuysen* sn. (BOL), 3030 (BOL), 3443 (BOL), 9540 (BOL), 29097 (BOL); *Ecklon & Zeyher 1720 (BOL); Fourcade* 3089 (BOL); *Gillett* 4244 (BOL); *Haynes* 362 (NBG, PRE); *Hennecart* 54 (BOL); *Kerfoot* 5397 (NBG, PRE); *Leighton* 12 (BOL); *Levyns* 482 (BOL), 2918 (BOL), 3016 (BOL),4061 (BOL), 4091 (BOL), 4776 (BOL), 7938 (BOL), 8056 (BOL), 9141 (BOL), 11634 (BOL); *Manson* 130 (NBG, PRE); *Maquire* 155 (BOL); *Parker* 3717 (BOL); *Pillans* 7358 (BOL), 9292 (BOL); *Rodin* 3091 (BOL); *Stephens* 7125 (BOL); *Stokoe* 7260 (BOL); *Thompson* 176 (NBG, PRE); *Van Niekerk* 787 (BOL); *Van Wilgen* 162 (NBG, PRE); *Whitman* sn. (BOL); *Wolley Dod* 5 (BOL).

4. C. heterophylla Weim.

The fresh specimens *Karin Behr* sub *Fellingham* 1638 (NBG) and *Jane Forrester* sub *Fellingham* 1640 (NBG, BOL), were examined in the early Spring of 1994. Six field trips were undertaken between the 3rd of January 1995 and the 22nd June 1995 to the Harold Porter Nature Reserve in Betty's Bay, to study this species in situ and to collect the following fresh specimens for further study: *Fellingham* 1647 - 1652 (NBG), 1654 - 1658 (NBG), 1662 (BOL), 1663 (NBG), 1668 (NBG), 1673 (NBG), 1674 (BOL), 1675 (NBG), 1676 (BOL), 1677 (NBG). Sketches are from *Forrester* sub *Fellingham* 1640 (NBG, BOL).

Herbarium specimens examined:

Boucher 209 (NBG, PRE); *De Vos* 624 (NBG), 1213 (NBG); *Ebersohn* 15/68 (NBG); *Esterhuysen* 13677 (BOL), 29003 (BOL, NBG); *Grobler* 20181 (NBG); *Kruger* 801 (NBG); *Leighton* 13 (BOL); *Levyns* 7789 (BOL), 7795 (BOL), 8095 (BOL); *Marloth* 14106 (NBG); *Stokoe* 405 (BOL, PRE, SAM), 7264 (BOL), 9048 (BOL), 17238 (BOL), SAM 61486 (NBG, SAM), SAM 59988 (NBG, SAM); *Van der Merwe* 847 (NBG).

5. C. odorata L. f.

Fresh material was collected during field studies on this species, from a population around the two dams above the grounds of the Lord Charles Hotel in Somerset West, over the flowering season of January to June 1995. These specimens were *Fellingham* 1660 (NBG), 1664 (BOL, NBG) & 1678 (BOL, NBG & PRE).

Herbarium specimens examined:

Bolus 19854 (BOL), 19855 (BOL); *Compton* 14374 (BOL), 15589 (BOL); *Cooper* 1451 (BOL); *Dickin* 83 (BOL); *Esterhuysen* 1831 (BOL), 15311 (BOL), 19430 (BOL), 23890 (BOL), 29064 (BOL), 30049 (BOL), 33509 (BOL), 33759 (BOL); *Fourcade* 24 (BOL); *Leighton* 2977 (BOL); *Levyns* 6466 (BOL); *Loubser* 825 (BOL); *Michell* BOL16091 (BOL); *Nel & Boucher* 73 (BOL, NBG, PRE, K); *Parker* 3663 (BOL); *Paterson* 2015 (BOL); *Sims* 2514 (BOL); *Stokoe* sn. (BOL).

6. C. arborea Marl.

Field work was done on the two populations on the Nieuweveldberg escarpment, at Beaufort West and fresh material taken for study were *Fellingham* 1624 (MO, NBG, PRE all female) and 1625 (BM, NBG , PRE all male & female).

Herbarium specimens examined:

Acocks 18621 (BOL male & female, K male & female, NBG male); *De Villiers* sn. (NBG immature female); *Marloth* 3907 (BOL female, K male), 9730 (NBG male & female), 9770 (NBG female, PRE female); *Moffett & Steensma* 4067 (NBG male); *Oliver* 10054 (BOL, K, MO, NBG, PRE, S all female); *Shearing* 893 (PRE female).

7. C. conifera E.G.H. Oliv. & Fellingham

Fresh material of the type, *Oliver* 10055 (BOL, K, NBG, PRE, all male & female) was examined and sketched. The type locality, the eastern end of the Anysberg in the Ladismith district, was visited and more fresh material, *Fellingham* 1531 (NBG female), collected for examination in the herbarium.

Herbarium specimen examined:

Oliver 9730 (NBG, PRE, S all female); *Van Wyk* 1072 (NBG female).

8. C. dichotoma Fellingham

Field work on this species was done in September 1995, November 1995, November 1996, and October 1997, on the farm Papkuilsfontein in the Lokenberg area of Namaqualand. Specimens were collected on all of these occasions. The fresh specimens studied and sketched were *Fellingham* 1684 (BOL, NBG, K, PRE) and *Fellingham* 1689 (BOL, NBG, K), collected on the 27th September 1995 and the 16th November 1995 respectively.

Herbarium specimens examined:

Fellingham 1702 (BOL, NBG both male & female, PRE, K both male); 1705 (BOL, NBG, PRE); 1706 (BOL); 1707 (BOL); 1708 (BOL); 1709 (BOL, NBG, PRE); 1710 (BOL); 1711 (BOL); 1712 (BOL); *Pretorius 396* (BOL, K, MO, NBG, PRE); *Yvette Van Wyk* 626 (NBG); *Von Willard* sn. (NBG).

In spite of the fact that Weberling's (1989) new terminology had been used to describe the inflorescence in *C. conifera* (*Oliver & Fellingham* 1994), I have been reluctant to use it in this paper, since his definition of a raceme or botrys (botryum?) as having 'clearly developed internodes' and 'stalked flowers', seems to preclude its application to the short shoot inflorescence typical in the genus *Cliffortia*. It would appear that Weberling's earlier (1983) definition of long shoots and short shoots in terms of their respective functions, is more appropriate to the subject of this paper. I therefore, prefer to define the inflorescences in terms of short shoots as well as the modern terminology.

Chapter 3: RESULTS

1. Cliffortia nivenioides Fellingham

This species is known from the type locality only: a very discreet locality on an open sunny marsh at an altitude of almost 2000 m, north of Blesberg in the Swartberg Mountains.

The general appearance of this small shrub is that of a compact bunch of long branches emerging from a central point. These long branches are themselves sparsely branched to totally unbranched. The leaves are arranged imbricately on short shoot to form flat slightly elongated fans. The combined effect resembles a species of the genus *Nivenia* Vent. (Iridaceae) (Figure 1.1A).

Flowers occur on the apical short shoots only, or rarely also on one or two lateral short shoots just below the apex. The subtending leaves are ordinary vegetative leaves, bilaterally flattened and closely arranged on the short shoots, with the leaf sheaths imbricate, completely obscuring the internodes of the short shoot. (Figure 1.1A). As these subtending leaves are not modified in any way, they are not bracts. This is a significant factor in the interpretation of the inflorescence structure.

The male flowers occur together with the female flowers on the same short shoots, but in the lower and therefore older leaf axils. The young female flowers are borne singly and totally hidden in the axils of the leaves, causing fertile plants that had already shed their male flowers to be mistaken for sterile.

Being more mature and having larger calyx lobes and protruding stamens, the male flowers are more readily visible than the totally hidden, immature female flowers. (Figure 1.1A & C). This discrepancy in developmental stages between male and female flowers, would exclude the possibility

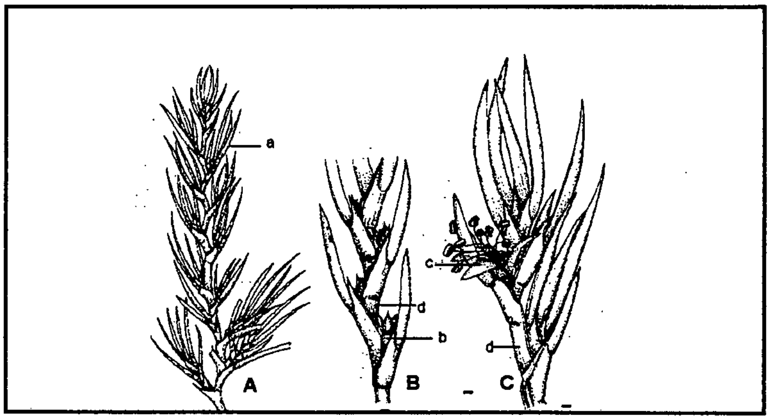

Fig. 1.1 A-C: ***Cliffortia nivenioides:*** **A**, long shoot bearing short shoots with female flowers hidden in axils of leaves; **B**, fruit-bearing long shoot, developed out of short shoot; **C**, short shoot with lower node elongating and lower leaf axil bearing male flower. **a**, short shoot with female flowers hidden in leaf axils; **b**, fruit; **c**, male flower; **d**, visible internodes. Drawn after Inge Oliver. *Viviers & Vlok* 470 (BM, BOL, K, MO, P, PRE, NBG) Scale bars = 1 mm.

of self fertilization.

The fertile short shoot in the axil of a vegetative leaf, on a long shoot, appears to be the inflorescence (Figure 1.1A & 1.2A: i1). The presence of vegetative leaves however, constitutes it a vegetative shoot. On this vegetative short shoot, the larger more visible male flowers are borne in the older (lower) leaf axils. The female flowers occur above the male flowers in younger leaf axils and are totally hidden at this stage (Figure 1.1A: a). It is only after a significant change has taken place in the short shoot axis, that the female flowers become

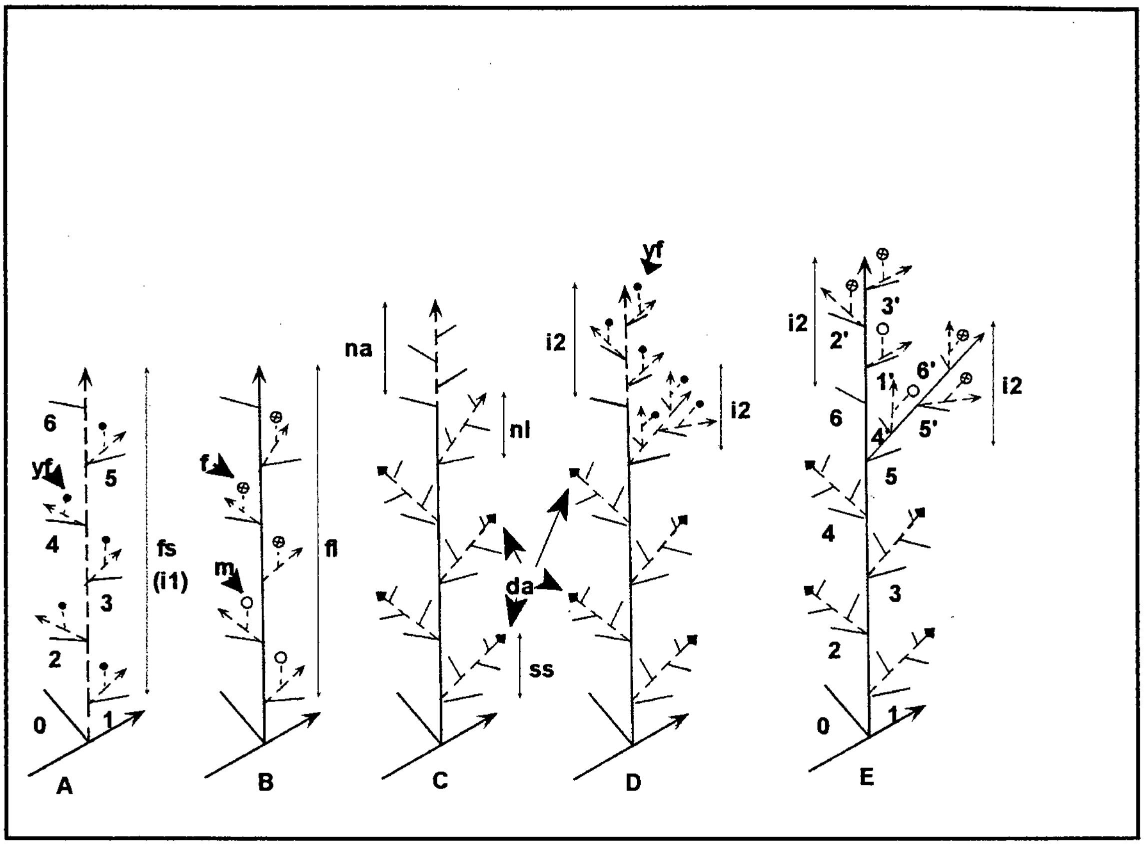

Fig. 1.2A - E, Longitudinal diagrams of inflorescence and branch development, covering two fertile seasons spanning a vegetative season, in *C. nivenioides*. **A,** young fertile short shoot of the first fertile season with young single-flowered inflorescences; **B,** same as A, matured: a long shoot with mature flowers; **C,** vegetative stage : a branch consisting of a long shoot bearing new short shoots; **D,** second fertile season's fertile short shoot: the apical and one lateral short shoot; **E,** same as D, matured: aical and lateral long shoots: lateral long shoot to become vegetative branch; 0, subtending leaf on main branch; 1 - 6, subtending leaves of first season's inflorescence; 1' - 6', subtending leaves of second season's inflorescences; yf, young flower; fs, fertile short shoot; f, female flower, m, male flower; fl, flowering long shoot; na, new apical short shoot; nl, new lateral short shoot; da, dormant apical buds; ss, sterile short shoot; i1, fertile shoot of first season: short shoot becoming long shoot; i2, fertile shoot of second season: short shoot becoming long shoot. Broken lines = axes of short shoots.

visible. The lengthening, in ascending order, of the hitherto very short internodes of the short shoot with imbricate leaves, changes it into a long shoot with distant leaves. This clearly reveals the true nature of this short shoot as equivalent to the vegetative long shoots supporting the inflorescences encountered in other species. With the leaves no longer imbricate the flowers are fully revealed, the lower male flowers first and afterwards the developing female flowers, which by this time have developed into fruits. (Figure 1.1B, 1.2B).

At the end of the flowering season the male flowers and the fruits are shed and the vegetative stage (Figure 1.2C) is entered. This is marked by two events. Through proliferation of the apical bud of the newly formed long shoot, a new apical short shoot (na), is formed, and new lateral short shoots (nl) develop in the axils of the leaves, which subtended the past season's flowers. While appearing to replace the single flowers, these lateral short shoots are in fact, the proliferation shoots of the minute single-flowered inflorescences of the recent flowering season. Thus a new branch is formed, consisting of a long shoot axis that originated as the axis of the flowering long shoot (fl), the apical proliferation (short)shoot (na), and lateral short shoots (nl) that proliferated from the lateral single-flowered inflorescences. Most of these newly formed short shoots on the branch, remain vegetative and do not undergo any further vegetative growth. Their apical buds have become dormant. Only a small number near the apex of this vegetative branch develop further, viz. the new apical short shoot (na) and the uppermost new lateral short shoot (nl). These become the flowering short shoots or pseudo-inflorescences of the second season (Figure 1.2D: i2).

The second flowering season starts when the new apical short shoot (na) and the new lateral short shoot(s) (nl), become the new flowering short shoots (i2). Their imbricate leaves (1' - 6') become the subtending leaves for the new single-flowered inflorescences (Figure 1.2C, D & E). As in the previous fertile stage (Figure 1.2A: fs & B: fl), these fertile short shoot(s) change from short shoots with imbricate leaves, into long shoots with distant leaves as they mature (Figure 1.2D: i2 & E: i2).

The number and positions of the long shoots thus formed, are determined by the number and positions of the short shoots involved in flower-bearing. With only the apical short shoot and one lateral involved, the result will be one apical long shoot and one side branch (Figure 1.2D & E). As before, the next stage of development is the shedding of the flowers leaving the new long shoots with their now no longer imbricate leaves (1' - 6'), ready to subtend a new generation of short shoots and thus becoming the new branches.

Branching occurs only where long shoots develop. The sparse vegetative branching pattern in this species, is thus directly linked to the structure of the fertile shoot (pseudo-inflorescence) of the previous fertile season, limiting the development of long shoots. Where only the new apical short shoot (na) develops into the new fertile shoot (i2), no side branch will develop, so that solely longitudinal growth takes place. It is only when one (or more) of the lateral short shoots (nl) are also flower-bearing, that lateral long shoots develop and branching occurs (Figure 1.2D & E).

Summary:

!. Viability of apical buds:

Every fertile short shoot retains a viable apical bud, while sterile short shoots have permanently inactive apical buds.

2. Position of flowers:

In every leaf axil that contains a flower in the fertile stage, a short shoot will develop in the vegetative stage. This apparent 'replacement' of the flowers with short shoots, seems anomalous unless the fact is kept in mind that the flowers are not terminal, but lateral on minute single-flowered short shoot inflorescences with apical buds which will proliferate only in the following vegetative stage.

3. Three types of short shoots:

Minute short shoots form the axes of the single-flowered inflorescences, in the axils of vegetative leaves on fertile short shoots.

Fertile short shoots occur on the apical regions of branches, give rise to the single-flowered inflorescences and retain their viable apical buds.

Sterile short shoots occur lower down on branches, remain short shoots through loosing the viability of their apical buds.

4. Subtending leaves:

The ordinary vegetative leaves subtend what appears to be single flowers but which are in fact, single-flowered inflorescences with e-bracteate flowers.

5. Short shoots and long shoots:

This species is marked by a preponderance of short shoots, of which only those that had been involved in flower-bearing develop into long shoots.

The only long shoots in this species are those that develop out of the fertile short shoots.

6. Sexuality of the plant:

Male and female flowers are borne together on the same short shoot, the males lower down on older nodes. The plants are, therefore, monoecious.

7. Branching pattern:

Branching is linked to the development of lateral fertile short shoots which occur in the apical zones of main (long shoot) branches only and is, therefore, sparse.

2. *Cliffortia crenata* L.f.

This species occurs on mountain slopes and plateaux at altitudes ranging from 1300 m in the northern, drier areas to 300 m in the Montagu area.

The plants appear to be totally without short shoots, being virgate, lanky shrubs to 2 m tall, branched in the upper parts only and that, very sparsely. At no time are any flowers visible. The two large leaflets are attached to the stem at an acute angle, completely enveloping it, so that, in order to examine the leaf axils for flowers, at least one of the leaflets have to be folded back or removed.

The inflorescence:

A primordial inflorescence is seen in figures 2.1G and 2.2A, as consisting of a pair of immature flowers (f), one slightly above the other, attached to a swollen basal structure (g), with an apical bud (c) between the two flowers. The flowers are subtended by small but unmistakably leafy elements (e). The size of the immature flowers relative to that of the inflorescence axis, facilitates the interpretation of the structures. It is quite clear that the flowers are borne on the swollen basal structure and not adjacent to it. In terms of the elements of a simple inflorescence consisting of a short shoot, the swollen basal structure is the inflorescence axis bearing two lateral, alternate flowers with the apical portion of the axis continuing beyond. In an inflorescence this much condensed the subtending leafy elements can be expected to be bracts rather than vegetative leaves.

A primordial inflorescence can develop into one of two types of mature inflorescences: a condensed type and a proliferating type.

The condensed type contains a single flower or a cluster of mature flowers, on a much condensed inflorescence axis without any apical proliferation. In a typical instance, three flowers were found in a cluster: the two lower ones, female and the one above, a male. These three mature flowers obscured the inflorescence axis and its ancillary vegetative parts viz. leaves or bracts. The two female flowers were much more advanced in development than the male. The one female was a fully developed fruit without calyx lobes while the other was a younger fruit with the calyx still in place. The male flower was still in the bud stage. (Figures 2.1A & 2.2B).

This inflorescence represents the matured form of the contracted primordial inflorescence, without any proliferation of the apical bud. The contracted axis is a short shoot bearing flowers of both sexes, laterally in the axils of bracts. The male flowers are always on the apical node(s). In this instance the flower-bearing short shoot is completely obscured by the large mature flowers (Fig.2.1A). This is contrary to the ease with which the structure of the primordial inflorescence can be seen because of the relatively small size of it's flowers (Fig. 2.1G) The diminutive size of the subtending leaves suggests that they would not develop into vegetative leaves but that, in this case, the male flowers are also subtended by bracts.

The proliferating type of mature inflorescence presents not only clusters of fruit and flowers, but has a proliferating apical bud which gives rise to a young vegetative shoot which eventually develops into a branch. When first encountered, this phenomenon was interpreted as a cluster of flowers sharing a leaf axil with a vegetative shoot. Closer examination however, revealed the shoot to be attached to the little group of fruit and flowers and not a separate structure as had been assumed on first sight. In fact, the shoot is the structure that originates in the leaf axil and the flowers are borne on the basal part of the shoot and not directly in the axil (Figure 2.1B & 2.2C).

Examining a typical shoot of this kind from the base upwards, the following observations can be made:

The lower two flowers are female and close to each other with their small imbricate subtending leaves completely covering the very short internodes. The next flower is female and followed by younger male flower(s). The internodes separating the flowers become increasingly longer upwards, but remain much shorter than those higher up on the vegetative part of the shoot (Figure 2.1B). The leaves subtending the basal female elements (fruits and / or flowers), show progressive development from the base upwards. The lowest are merely scale-like structures, consisting mainly of a narrow sheath without any stipules and with only the vestige of a blade attached directly to the sheath, without articulation. (Figure 2.1C). Above these are leaves in progressive stages of development from very small bracts with just the indication of stipules and a single articulating leaf blade (Figure 2.1D), to almost normal, small vegetative leaves with two leaflets (Figure 2.1E). These small leaves subtend the male flower(s) (Figure 2.1B:a). Above the male flowers the shoot becomes a normal long shoot with vegetative leaves. In occasional leaf axils near the apices of these vegetative shoots, small buds which could develop into secondary primordial inflorescences, are found (Figure 2.1F & 2.2C:pi).

The proliferating inflorescence consists thus of a basal flower-bearing short shoot (s sh) in which the apical bud proliferates into a distal long shoot (l sh) which will lengthen to extend beyond the subtending leaf to form the new branch (Figure 2.2). This type of inflorescence occurs less frequently than the contracted type in which no branch is developed.

A relatively small number of inflorescences, usually near the apices of the branches, proliferate thus. These then, are the only inflorescences that give rise to vegetative branches, as the formation of branches depends entirely on the occurrence of inflorescences with distal long shoot development. The sparseness of the branching pattern, resulting in the virgate growth form of this species, can thus be directly related to the small number of inflorescences that undergo these full changes (Figures 2.1B & 2.2C).

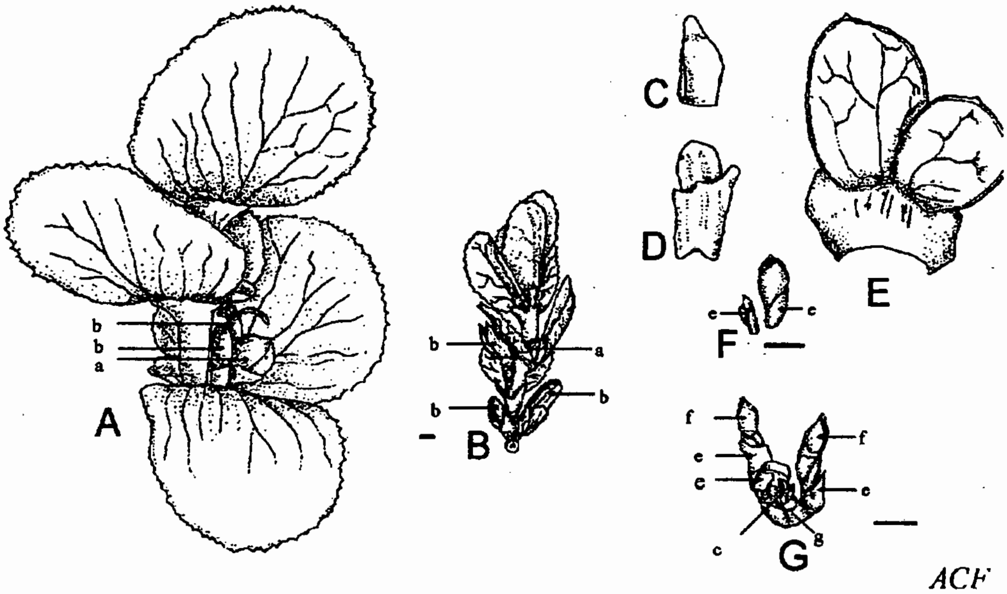

Fig. 2.1 A -H, *Cliffortia crenata*. A, portion of main branch with condensed inflorescence; **B**, proliferating inflorescence (branchlet from axil of vegetative leaf) ; **C, D & E**, subtending leaves, in ascending order, on branchlet B; **F**, apical growth point from axils of fourth and sixth leaves on branchlet B; **G**, primordial inflorescence(short shoot from axil of vegetative leaf near apex of main branch); a, male flower; b, female flower; c, growth point; d, side shoot; e, subtending leaves, f, flowers; g, contracted inflorescence axis. *Oliver* 10387 (NBG). Scale bars = 1 mm.

Summary:

1. Viability of apical buds :

Main stem:

Initial branching of the main stem takes place high up above ground level, after which its apical bud becomes dormant. Further linear growth is taken over by the sparse virgate branches.

Lateral:

In the condensed inflorescence, the apical bud of the short shoot becomes dormant, and no branch develops.

In the proliferating inflorescence the apical bud remains viable, giving rise to the vegetative branch and only after the vegetative branch has reached it's full potential and given rise to a side branch, does the apical bud become dormant.

2. Position of flowers:

All flowers are borne laterally. Female flowers occur on short shoots, and male flowers on short shoots and the basal parts of long shoots.

3. Two types of short shoots:

The characters of the two types of inflorescences are directly linked to the two types of short shoots that manifest themselves. The one in which the apical bud becomes dormant gives rise to the contracted inflorescence and the one with the viable apical bud, to the proliferating inflorescence.

4. Subtending leaves:

Male flowers occur in the axils of bracts in the case of the contracted inflorescence and ordinary, though somewhat modified, small vegetative leaves in the proliferating inflorescence. Female flowers occur in the axils of bracts.

5. Short shoots and long shoots:

In the contracted inflorescence, both male and female flowers are borne on the short shoot, the male flowers on the upper nodes. In the proliferating inflorescence, male flowers are borne on the transition zone between the basal female flower-bearing short shoot and the purely vegetative part of the long shoot, in the axils of small modified vegetative leaves.

6. Sexuality of the plant:

Male and female flowers are borne together in the same inflorescence, though the male flowers on higher (younger) nodes. The plants are thus monoecious; probably self-infertile because of difference in maturity of the flowers.

7. Branching pattern:

The contracted inflorescence is dedicated to flower-bearing and then discarded, without contributing anything to the vegetative structure of the plant. The rarer proliferating inflorescences, occurring near the apices of main branches, are the only sources of vegetative increase. This gives rise to a sparse branching pattern and a virgate plant.

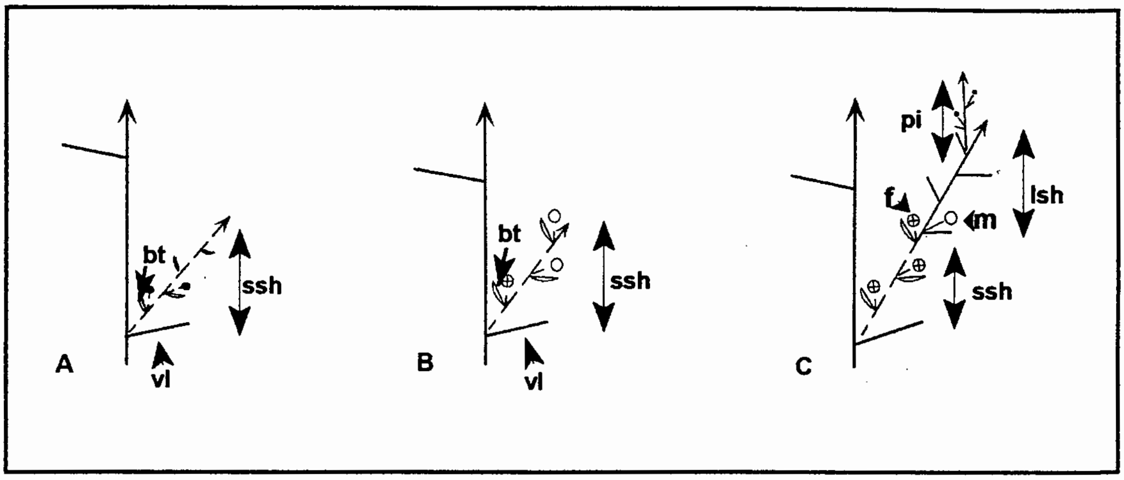

Fig. 2.2A - C, Longitudinal diagrams of inflorescences in different stages of development in *C crenata.* A, primordial inflorescence with immature flowers; B, mature contracted inflorescence with mature male and female flowers; C, Inflorescence with mature male and female flowers, vegetative branch and secondary primordial inflorescence; bt, bract; f, female flower; m, male flower; vl, vegetative leaf; ssh, short shoot; lsh, long shoot; pi, primordial inflorescence. Broken lines = axes of short shoots.

3. Cliffortia ruscifolia L.

This is a widespread and probably the most well-known species of *Cliffortia,* occurring in well drained habitats over a wide altitude range. It occurs in a great variety of vegetative forms from low sparse sprawling plants with yellowish green leaves, to erect bushy plants to 1.5 m tall and with grey/green leaves, from the same locality. The size and shape of the vegetative leaves are also very variable but always unifoliate and pungent.

The inflorescence structure in this species varies from the typical multi-flowered bracteose type, to the rare single-flowered form with the flower apparently subtended by an ordinary vegetative leaf. The latter type, could have been taken for the immature form of the inflorescence if it was not for the fact that the female element in it was a mature fruit (Figure 3.1A & P).

In essence the inflorescence is a short shoot, occurring in the axil of an ordinary vegetative leaf on a long shoot. Male and female flowers are borne singly in the axils of bracts, in a single inflorescence, usually with the female flowers below the males (Figure 3.1A & N).

Two distinct zones can be distinguished in the short shoot. The lower zone consists of around five vegetative leaves which graduate in form and size from long and narrow in the lowest leaf, to much shorter and wider in the highest. All of these leaves are typical vegetative leaves, plain with slightly hairy edges and nerves and sharp apical spinelets. With the leaves diminishing in length upwards, this zone seems to fit the description for Weberling's 'field of inhibition'. For such a small area of inhibition as is encountered here, the term inhibition zone seems appropriate. As seen in figure 3.1N, the leaves of this area are shed to reveal the fertile part of the inflorescence, a zone of imbricate bracts, each subtending a flower. The bracts are much shorter and more hairy than the leaves of the inhibition zone, and dentate to trilobate. The apical bracts are immature in some instances. All multi-flowered inflorescences contain male and female flowers in equal proportions (Figure 3.1A-G, N & 3.2A).

The apical buds of the mature inflorescence proliferate to form comas of young vegetative leaves, some with minute buds in their axils, on a developing long shoot. The appearance of this vegetative long shoot marks the onset of the new vegetative stage. This phenomenon can be defined in terms of Weberling's concept of 'late proliferation', except that he sets the prerequisite of a frondose inflorescence for the use of this term. It does otherwise fit the requirement of marking the return of the 'inflorescence apex to the vegetative condition'. In spite of the bracteose character of the inflorescence, I propose the use of the term proliferation zone for the early stage of development of the long shoot (Figure 3.1A: pz, H-K & 3.2B: az, C: ls).

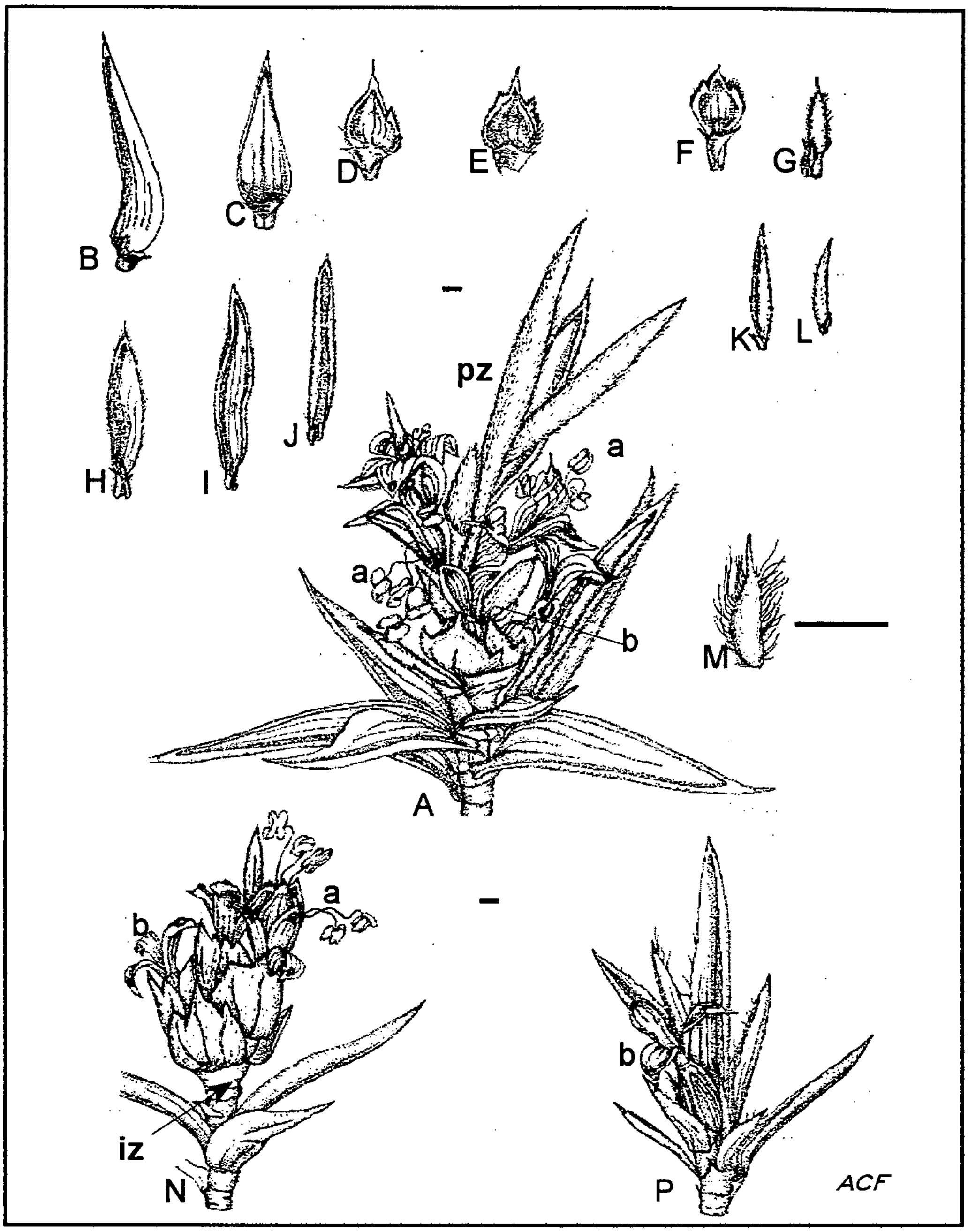

Fig. 3.1A-P, ***Cliffortia ruscifolia***; **A, N, P**, inflorescences from three different specimens; **B,C**, vegetative leaves from just below inflorescence; **D - M**, leaf elements removed from A in ascending order; **D, E, F, G**, bracts subtending flowers in inflorescence; **H, I, J, K, L**, leaves of proliferation zone; **M**, growth point of proliferation zone; a, male flower; b, female flower; iz, inhibition zone; pz, proliferation zone. *Oliver* 10387 (NBG). Scale bars = 1 mm.

With the appearance of the proliferation zone, the vegetative stage is entered. At the same time, or in some instances, before this event, the leaves of the inhibition zone, are shed, followed by the shedding of the flowers and their subtending bracts (3.1N, 3.2B & C) .

The short shoots are thus left bare with the short internodes, (which do not elongate), permanently visible. The proliferation zones are thus the entire source of vegetative growth. These then develop into long shoots with proximal zones of bare short internodes as the only indications of the sites of the old inflorescences. Though these zones are a permanent feature of the basal (proximal) portions of all branches thus derived, they do not contribute any further to their development (Figure 3.2B-D).

As the fertile stage is characterized by the development of short shoots, the vegetative stage is characterized by the development of long shoots proliferating out of the short shoots (Figure 3.2B, C).

Potentially every short shoot could develop into a vegetative branch. Furthermore, all the leaves on a long shoot could become subtending leaves for the next fertile season's short shoots (Figure 3.2D).

It is, however, usually only a random number of leaves that develop short shoots in their axils. Of these short shoots there is again only a random number that give rise to long shoots .

Summary:

1. Viability of apical buds:

Although a large proportion of the short shoots have viable apical buds and could go on to generate distal long shoots after flowering, some do not. The pattern and frequency of the occurrence of dormant apical buds, seem to be random. There is a tendency for the short shoots with dormant apical buds to eventually shrivel and fall.

2. Position of flowers:

All flowers occur laterally on short shoots.

3. Two types of short shoots:

No distinction between male and female flower-bearing short shoots exists. The difference is in the eventual development into a long shoot in the one case and the abortion of the remains of the inflorescence in the other.

4. Subtending leaves:

The leaves subtending both male and female flowers are bracts.

5. Short shoots and long shoots:

Short shoots are essentially inflorescences while long shoots represent vegetative growth. The remains of the short shoot is a permanent feature of the proximal part of the long shoot.

6. Sexuality of the plant:

Male and female flowers occur together in the same inflorescence, usually with the female flowers below the males. The plants are, therefore, monoecious.

7. Branching pattern:

There is an obvious link between the position, type and development of the inflorescences and the pattern of vegetative branching, through the alternating of the formation of short shoots in the axils of leaves on long shoots and the development of long shoots as the linear continuation of short shoots. The branching pattern is rich though random.

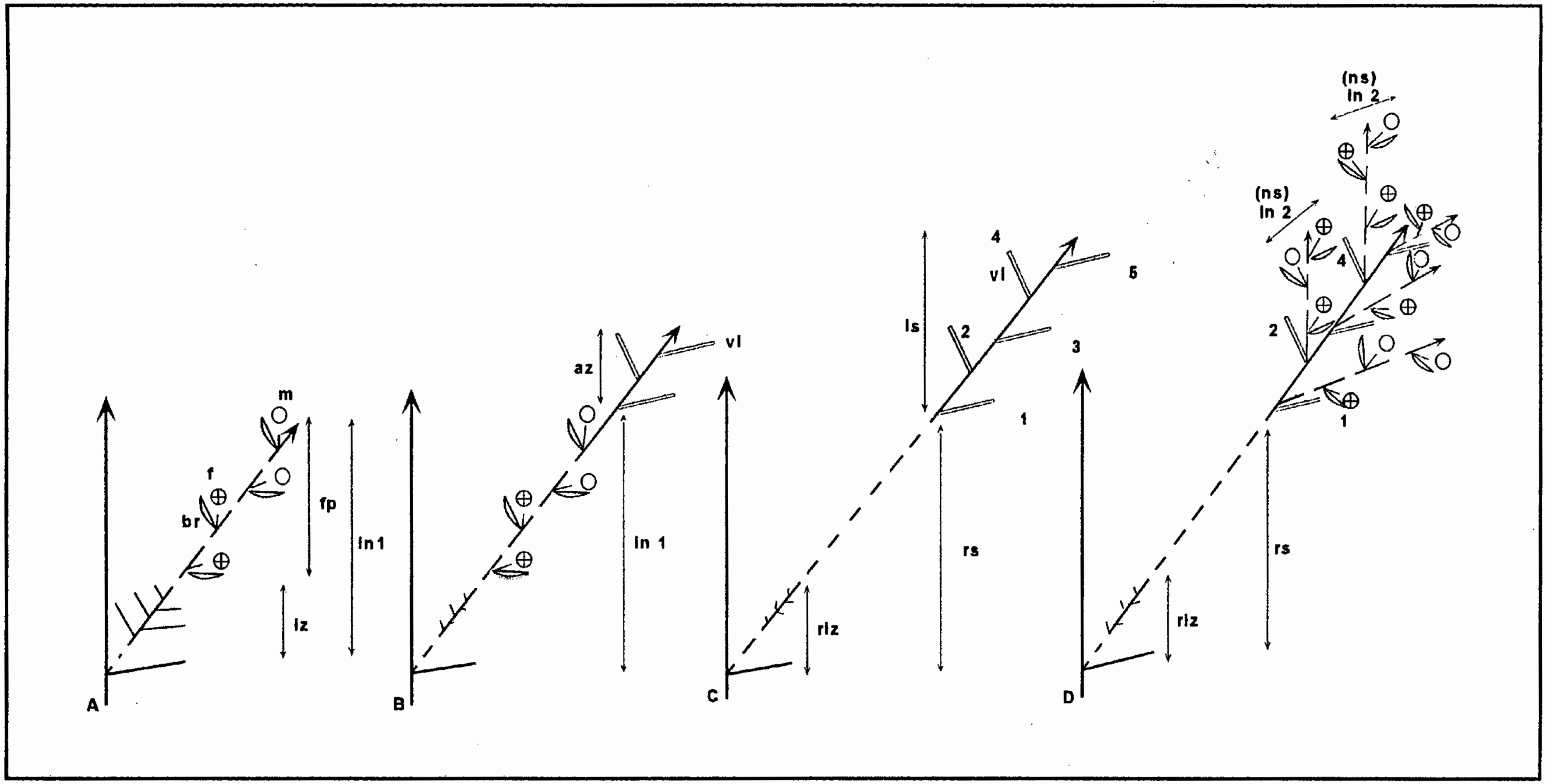

Fig. 3.2A-D Longitudinal diagrams of inflorescence development and related branches in ***Cliffortia ruscifolia.*** **A**, young inflorescence in axil of vegetative leaf on long shoot; **B**, mature inflorescence with proliferation of apical bud; **C**, vegetative stage: new branch consisting of remains of the short shoot (rs) plus new long shoot (ls); **D**, new inflorescences in axils of vegetative leaves on long shoot, constituting potential new branches developing as illustrated in B and C; m, male flower; f, female flower; br, bract; fp, fertile part of short shoot; iz, inhibition zone; in 1, inflorescence of first season; az, apical proliferation zone; vl, vegetative leaf; riz, remains of inhibition zone; ls, long shoot; rs, remains of short shoot; ins 2, inflorescences of second season; ns, new short shoot; 1 - 5, vegetative leaves on long shoot becoming subtending leaves for inflorescences of second season. Broken lines = axes of short shoots.

4. *Cliffortia heterophylla* Weimarck

This species is locally common in sunny situations near streams in the Betty's Bay area.

In the vegetative stage, the plants have the general appearance of saplings up to 3 m tall, with willow-like leaves and some secondary thickening of the

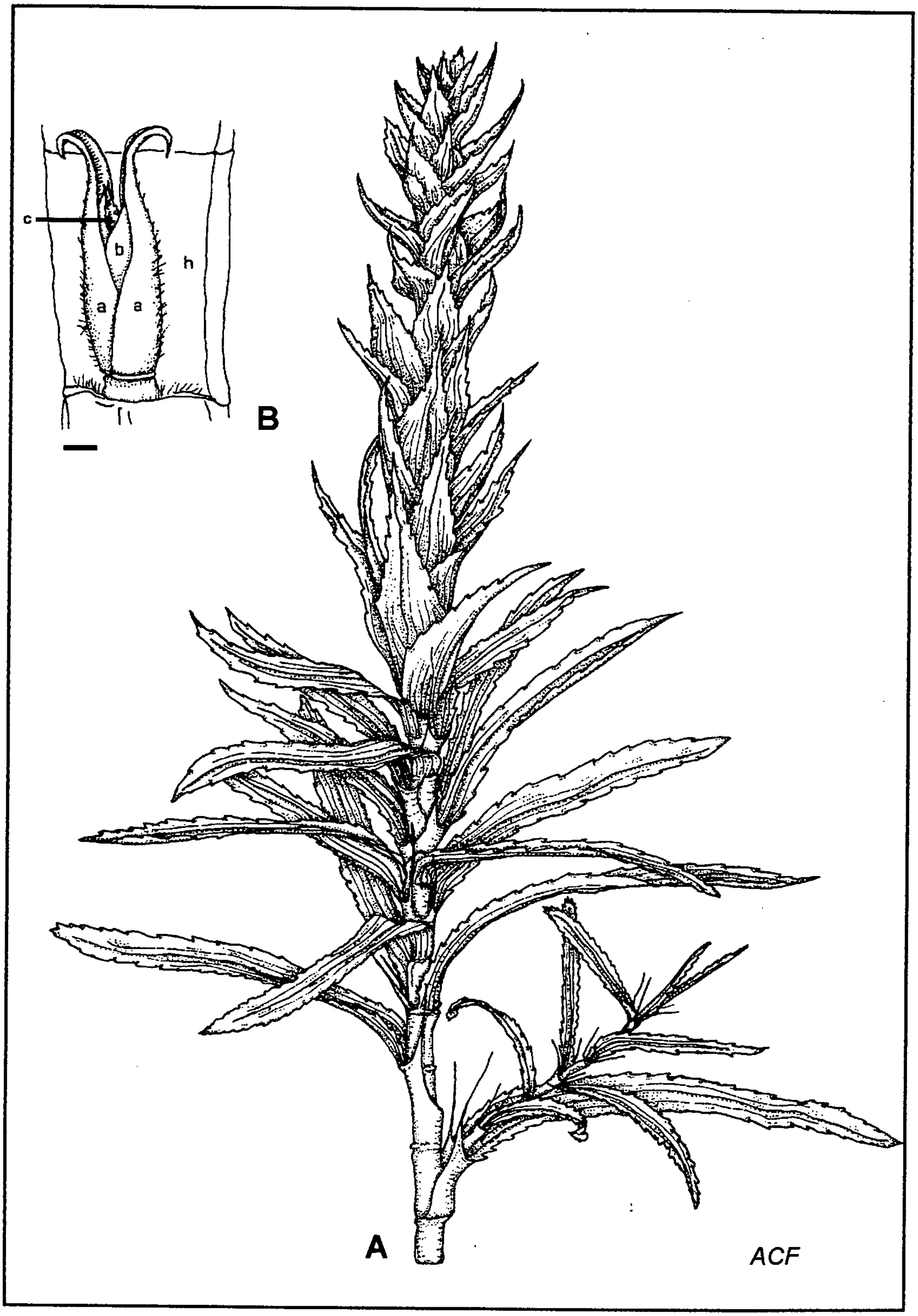

Fig. 4.1A & B, ***Cliffortia heterophylla*****;** **A**, female inflorescence on apex of main stem; **B**, female flower in situ on node (leaves removed); a, bracteoles, b, calyx lobes, c, stigma; h, internode. *Fellingham* 1640 (NBG). Scale 75%.

main stems. They are so unlike typical *Cliffortia*s that, during field trips in vegetative seasons, I had passed by the plants without recognizing them. With the differentiation of the leaves into two distinct forms in the spring, however, the plants become conspicuous even though no flowers, male or female, are visible at that stage. The apical cylindrical structures covered in imbricate, lanceolate-acuminate leaves quite unlike the normal vegetative leaves, are quite striking in appearance. Dissection of these cylinders revealed female flowers in the axils of the modified leaves, designating the apical cylinder, a female inflorescence and the modified leaves, bracts (Figure 4.1A & B).

Later in the same fertile season, two other plant forms can be recognized. One is an unmistakable bi-sexual form with male flowers patently obvious on ordinary vegetative branches just below the cylindrical female inflorescence, and the second is a form with male flowers only and totally devoid of any female elements viz. apical cylinder or female flowers. These findings seem to substantiate the idea of the dioecious state as the norm for *Cliffortia,* with the bi-sexual form as an anomaly.

Closer examination of fresh material, both in situ and after dissection, however, revealed that, that which had been taken as separate male and female plants with an occasional anomalous bi-sexual form, in fact represents normal developmental stages of the inflorescence, from the initial female stage, through the bi-sexual to the male stage. The inflorescence can, therefore, not be treated under two headings viz. male and female, as if these were separate entities, but has to be seen as the inflorescence undergoing profound changes as it develops out of the vegetative stage, through a full fertile cycle, ending in the new vegetative stage. Only minimal traces of the fertile stage, in the form of amplexicaul sheaths around the main axis of the plant, are left in the vegetative stage, after the shedding of the fugacious bracts. With the secondary thickening of the main stem, these sheaths also disappear as they are stretched and broken (Figure 4.2 mz, vz).

The bi-sexual inflorescence mentioned above, is in fact the true inflorescence, demonstrating all the different developmental stages in the form of recognizable zones, which are dealt with here in the chronological order of development, viz. female zone, male zone and the two vegetative zones: the inhibition zone and the proliferation zone. The longitudinal diagram (Figure 4.2) depicts all of these zones as one entity. This however, is the true state of affairs only a minority of cases. Usually the proliferation of the apical bud to form the apical proliferation zone (az), takes place only after the shedding of all sexual elements.

Female zone:

Apically on the main stem of a healthy plant, a single conspicuous cylindrical inflorescence emerges in spring. (Plants under stress, as those from which the apical inflorescences had been removed or those having their main stems constricted by twiners, do develop lateral inflorescences.) This cylinder is in essence, a short shoot up to 240 mm long, with the uppermost internodes about 1 mm long, gradually increasing in length to about 7 mm basally. All internodes of the short shoot are totally obscured by the lanceolate-acuminate bracts which are up to 60 mm long and 15 mm wide. In the larger part of the inflorescences, the female flowers occur singly on very short asymmetrical structures. In the older (lower) part of the inflorescence, up to six flowers are borne on lateral short shoots, totally hidden by the imbricate bracts.(Figure 4.2 ls). The flowers are lateral on these short shoots, and subtended by leafy elements that are much smaller than, and different in shape to the normal vegetative leaves, and therefore, bracts (bt). The short asymmetrical structures bearing the single flowers higher up on the same inflorescence, can thus be interpreted as primordial short shoots. Such a short shoot has a fully viable apical bud while only the lowest node is mature enough to sustain a fully developed flower, without the bract being in evidence yet. At this stage, the inflorescence can be described as a dibotrys, with a central short shoot bearing lateral short shoots in the axils of its bracts; the lateral short shoots bearing flowers in the axils of their bracts.

The male zone:

Two events mark the onset of the development of the male zone. The hitherto short internodes of the apical short shoot of the main stem start lengthening, the lower ones first and then the others in sequence upwards. This results in the separation of the previously imbricate bracts to reveal the internodes, thus changing the short shoot into a long shoot. (Figure 4.2 mz)

At the same time, the apical buds on all lateral short shoots (ls), give rise to long shoots (ll), in sequence from below upwards. These lateral long shoots lengthen and male flowers (m) develop on their distal parts, while the female flowers (f) on the proximal short shoot, mature into fruits before dropping off, starting with the lowest, then involving those higher up, again in ascending order. (Figure 4.2 mz)

The vegetative zone:

The formation of the vegetative zone is initiated by the shedding of the male flowers and any fruits that might still be present, leaving the remains of the lateral short shoot (rls) in the form of a region of short internodes interspersed with ridged nodes, on the proximal part of the branch (br). This is accompanied by the loss of the bracts (ib) on the main stem, leaving their remains (rb), the leaf sheaths which are eventually destroyed by secondary thickening of the main stem. Thus the vegetative zone (vz) comes into being, and develops upwards as the fruit and flowers mature and are shed. With the shedding of the last flower, the vegetative zone spreads to envelop the whole of the inflorescence, reducing it to a framework of newly formed vegetative branches. With this, the vegetative stage has been entered (Figure 4.2 vz).

The proliferation zone:

To complete the vegetative stage, one more change has to take place. The apical proliferation zone (az) has to come into being. This is achieved by the proliferation of the apical bud of the main inflorescence axil which is also the main stem, to give rise to an apical long shoot with vegetative leaves. In the axils of the vegetative leaves (vl) of this zone, purely vegetative branches (vbr) develop. These consist of long shoots only, without any remains of lateral short shoots on them as in the case of the branches originating in the inflorescence and are shorter than the side branches originating in the inflorescence (Figure 4.2 az).

The apical proliferation zone thus gives rise to the only purely vegetative growth of the plant. Proliferation of the apical bud can take place early in some instances, producing a coma above the apical cylindrical female zone (Figure 4.2 az & fz). Normally this occurs only after the vegetative zone is fully developed and the inflorescence has disappeared completely.

The inhibition zone:

The vegetative stage ends when the apical bud produces the new apical cylinder of imbricate bracts, marking the onset of the following fertile stage. This places the old apical proliferation zone directly below the new inflorescence. The youngest (apical) branches of the proliferation zone, will still be relatively short when the new inflorescence starts developing. This can be interpreted as that the old apical proliferation zone, becomes the inhibition zone of the new inflorescence (Figure 4.2 iz).

Summary:

1. Viability of apical buds:

Main stem:

The apical bud of the main stem remains viable throughout life. This bud is the main source of linear growth. The activity of this bud is interrupted by periods of restricted linear growth when the apical short shoot inflorescence is produced and resumed at the initiation of apical proliferation.

Lateral:

The apical bud of the lateral short shoot remains active till the branch is fully formed. Lateral growth of the plant does not continue indefinitely.

2. Position of flowers:

The female flowers occur in the axils of bracts on the node(s) of lateral short shoots and not directly in the axils of the imbricate bracts of the apical short shoot as was initially supposed. This fact redefines these female flowers as lateral and not terminal. Male flowers are lateral on single-flowered inflorescences in the axils of vegetative leaves.

3. The two types of short shoots:

The internodes of the female flower-bearing lateral short shoots lengthen somewhat in the fruiting stage, but are always significantly shorter than the internodes in the male flower-bearing lateral long shoots. This makes the lateral short shoot a permanent feature of the proximal part of the branch. In contrast, the apical short shoot of the female zone, becomes a long shoot through the lengthening of the internodes .

4. Two types of subtending leaves:

The male flowers occur singly and apparently directly in the axils of ordinary vegetative leaves. However, the fact that the subtending leaves are vegetative, indicates that what appears to be a single flower, is in fact a single-flowered inflorescence with the male flowers e-bracteate. The female flowers are borne in the axils of bracts.

5. Short shoots and long shoots:

Female flowers, are always associated with the presence of short shoots and male flowers with long shoots which develop out of the short shoots.

6. Sexuality of the plant:

Contrary to expectations, this plant has been found to be monoecious with the one inflorescence undergoing profound changes from an overtly female stage, through an apparently 'anomalous' bi-sexual stage to an overtly male stage. The bi-sexual stage in fact, reflects the true character of the inflorescence.

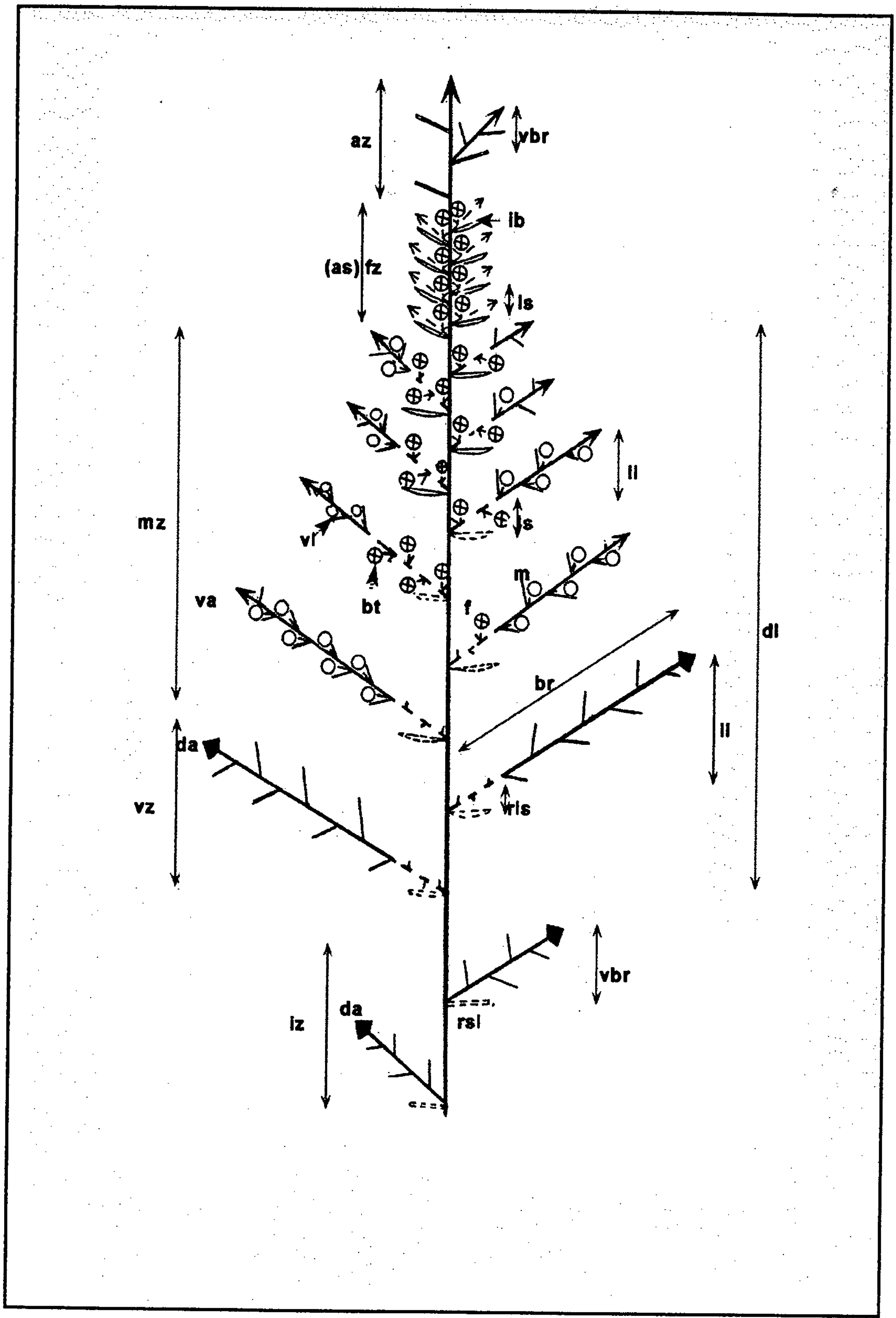

Fig. 4.2 Longitudinal diagram of inflorescence in ***Cliffortia heterophylla***. **az**, apical zone; **fz**, female zone; **mz**, male zone; **vz**, vegetative zone; **iz**, inhibition zone; **as**, apical short shoot; **ls**, lateral short shoot; **ll**, lateral long shoot; **rls**, remains of lateral short shoot; **dl**, developing main axis long shoot; **f**, female flower; **m**, male single-flowered inflorescence; **ib**, imbricate bract; **rb**, remains of imbricate bract; **bt**, bract; **br**, branch; **vbr**, vegetative branch; **da**, dormant apical bud; **vb**, viable apical bud. Broken lines = axes of short shoots.

7. Branching Pattern:

The vegetative branching pattern in this species is determined by the relative positions and developmental histories of the two types of short shoots present. The changing of the apical short shoot into a long shoot, and the proliferation of the main stem during the vegetative stage, place the focus of linear growth on the main stem which accounts for the remarkable growth rate with considerable secondary thickening, seen in this species. The second type of short shoots, the lateral short shoots, occur in the proximal parts of the side branches and though never developing into long shoots by internodal lengthening, do proliferate into much thinner and unbranched long shoots, resulting in side branches with limited linear growth. Resulting from this emphasis on the linear growth of the main stem while the branches increase in number rather than in length, is the typical, somewhat pyramidal, sapling-like form of the plant.

5. Cliffortia odorata L.f.

Dense stands of this species occur on the banks of rivers and dams in the south-western, southern and south-eastern coastal districts, usually at low altitudes but also up to 1000 m on Table Mountain.

The upright shrub is up to 2 m tall with the main stems slightly zig-zagging at the nodes, where the branches originate. This irregularity develops as a result of the displacement of the stem by the enlarging highly condensed inflorescences and the subsequent development of the branches in the axils of the amplexicaul leaves at these nodes.

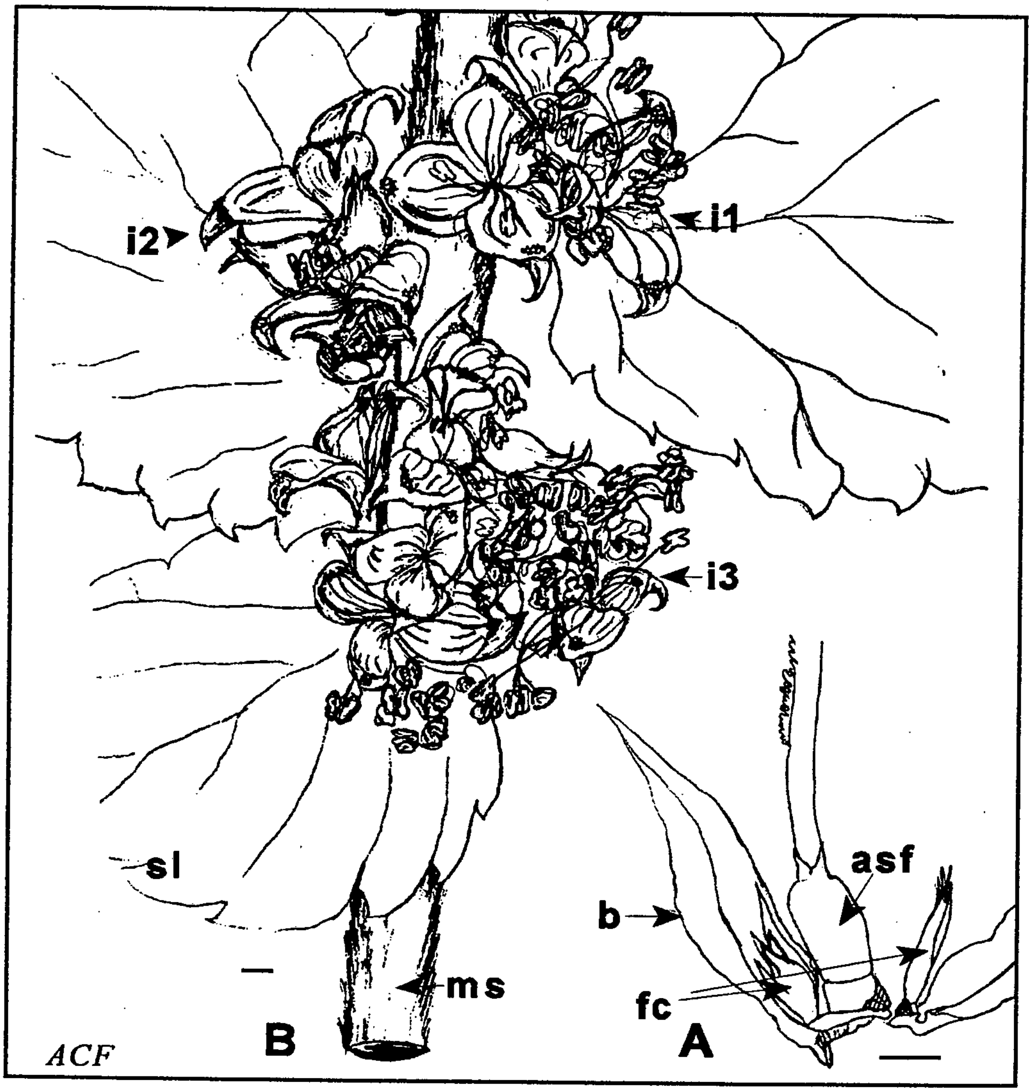

Fig. 5.1A & B. Inflorescences of *C. odorata.* **A,** young, apparently single flowered, inflorescence with central female flower ; **B,** three inflorescences consisting of clusters of flowers of both sexes; asf, apparently single flower; fc, flower cluster; b, bracteole; sl, subtending leaf; ms, main stem; i1, inflorescence 1; i2, inflorescence 2; i3, inflorescence 3.

The young inflorescence first appears as a single flower in the axil of a young leaf near the tip of a main stem or branch. This single flower is soon joined on the broad flower base which is the primordial inflorescence axis, by small clusters of much younger flowers with their bracts and bracteoles, developing between the first flower and it's bracteoles, thus causing the first flower to appear e-bracteate (Figure 5.1A).

These inflorescences are subtended by vegetative leaves, and develop into clusters of flowers of both sexes. Each cluster is composed of several sub-clusters, each subtended by a bract-like highly modified and extended membranous leaf sheath without a leaf blade. The individual flowers are interspersed with membranous bracts in varying states of development, with an occasional e-bracteate flower. The sub-clusters are implanted onto a flattened disc, the condensed inflorescence axis, by means of short stalks. Removal of the sub-clusters reveals the discreet implantation sites left on the disc. In the centre of an occasional inflorescence in this stage of development, a small raised area in the shape of a pyramid occurs. This pyramid is the apical bud of the condensed inflorescence axis, starting to proliferate (Figures 5.3A & 5.4A).

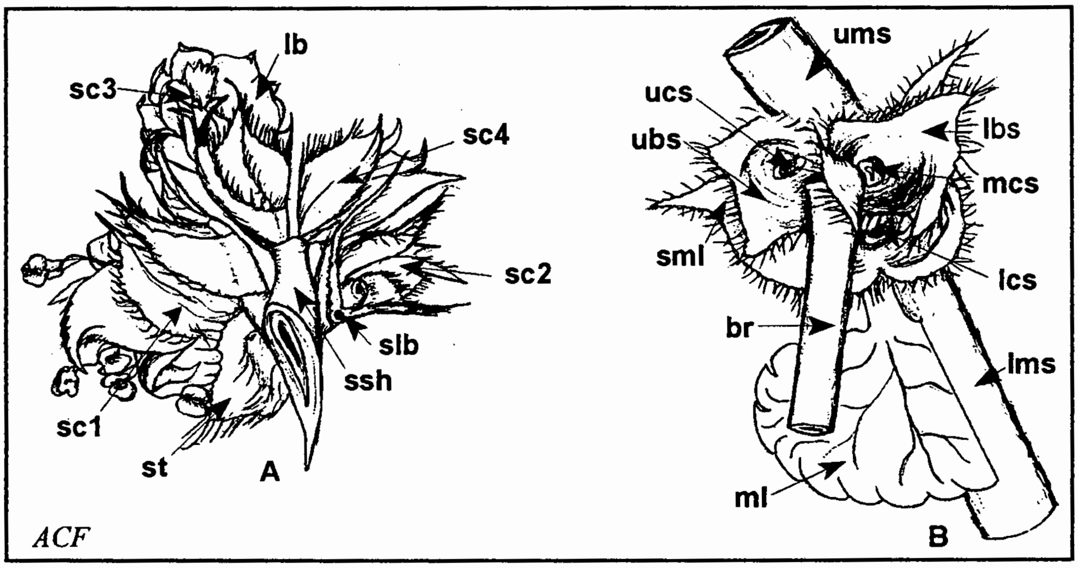

Fig. 5.2A & B.
Mature inflorescences of ***C. odorata***; **A**, proximal side of an inflorescence consisting of four sub-clusters and a vegetative short shoot separating these into two groups; **B**, compact inflorescence with branch (flowers and bracts removed); sc1 - 4, subclusters in order of development; lb, leaf blade; slb, scar of leaf blade; ssh, vegetative short shoot; ums, upper main stem; ucs, upper cluster scar; ubs, upper bract-like sheath; sml, stipule of leaf on main stem; br, branch; ml, leaf on main stem; lms, lower main stem; lcs, lower cluster scar; mcs, middle cluster scar; lbs, lower bract-like sheath.

In a significant proportion of inflorescences further changes follow, culminating in the production of a central branch in each inflorescence. In some cases the central pyramidal section of the initially much condensed inflorescence axis, develops into a very short vegetative shoot with one or two of the sub-clusters attached to it, thus separating these sub-clusters somewhat from the rest of the inflorescence. At the same time vegetative leaf blades develop on the sheaths subtending the sub-clusters, thus marking the nodes in the condensed inflorescence axis more clearly (Figure 5.2A & 5.4B). This interspersing of partial inflorescences with vegetative shoots results in the formation of a branch complete with small lateral inflorescences (Figure 5.4C).

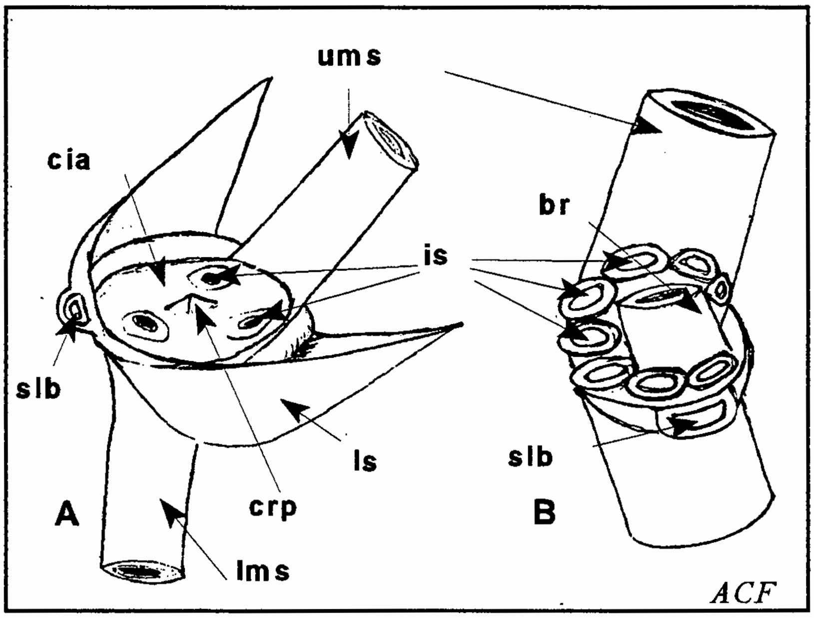

Fig. 5.3A & B: Semi-schematic drawings of the implantation sites of two compact inflorescences (flower clusters and leaf blades of subtending leaves removed) in ***C. odorata***. A, young inflorescence at onset of apical proliferation; B, mature inflorescence with fully developed branch; cia, condensed inflorescence axis; slb, scar left by leaf blade; lms, lower main stem; ums, upper main stem; crp, central raised pyramid, indicating onset of proliferation; ls, leaf sheath; br, branch; is, implantation scar of sub-cluster.

More often though, the composite cluster remains closely compact when the apical bud proliferates above the sub-clusters, generating a new branch with the amplexicaul leaf sheaths subtending the individual sub-clusters, still clasping it in maturity (Figure 5.2B). In large mature inflorescences with the central branch well developed, the implantation sites of the sub-clusters are so numerous as to be closely packed around the base of the branch, in a distinctly spiraling pattern (Figure 5.3B). This closely compact inflorescence with the apical proliferation giving rise to a branch, represents the basic structure of the typical inflorescence with the clear distinction between the production of short shoots, or as in this species, a system of short shoots, associated with the fertile stage and the long shoot formation of the vegetative stage (Figure 5.4A).

With two highly modified short shoots viz. the primary inflorescence axis as a flattened disc and the secondary axis as the stalk to a sub-cluster of flowers, the inflorescence can be defined as a double raceme or a dibotrys. The arrangement of these sub-clusters (dibotrya) within the total inflorescence is, however, not a fixed state. As seen above, in the instance of vegetative shoots and leaves developing in the inflorescence, a certain degree of plasticity exists, allowing the initially compact inflorescence to become more open (Figure 5.2A).

Summary:

1. Viability of apical buds:

The apical bud of the condensed inflorescence axis remains viable though inactive during early development of the inflorescence. The apical bud of the axis of the sub-cluster is only viable as long as flowers are being generated. In a single inflorescence, the activity of these two buds can alternate.

2. Position of the flowers:

The condensed nature of the inflorescence axis precludes the determination of the position of the flower. The clusters, however, occur in a spiral around the main branch (Figure 5.3B).

3. Types of short shoots:

The primary short shoot is the usually permanently condensed inflorescence axis with a viable apical bud that can, however, proliferate into a vegetative branch. The secondary short shoot is the permanently condensed axis of the sub-cluster which does not proliferate.

4. Subtending leaves:

A vegetative leaf subtends the inflorescence. A reduced and modified leaf sheath subtends the sub-cluster. A membranous bract subtends the individual flower. An occasional flower is e-bracteate.

5. Short shoots and long shoots:

The first order short shoot, or condensed inflorescence axis, proliferates into a long shoot, which is the axis of the vegetative branch. The second order

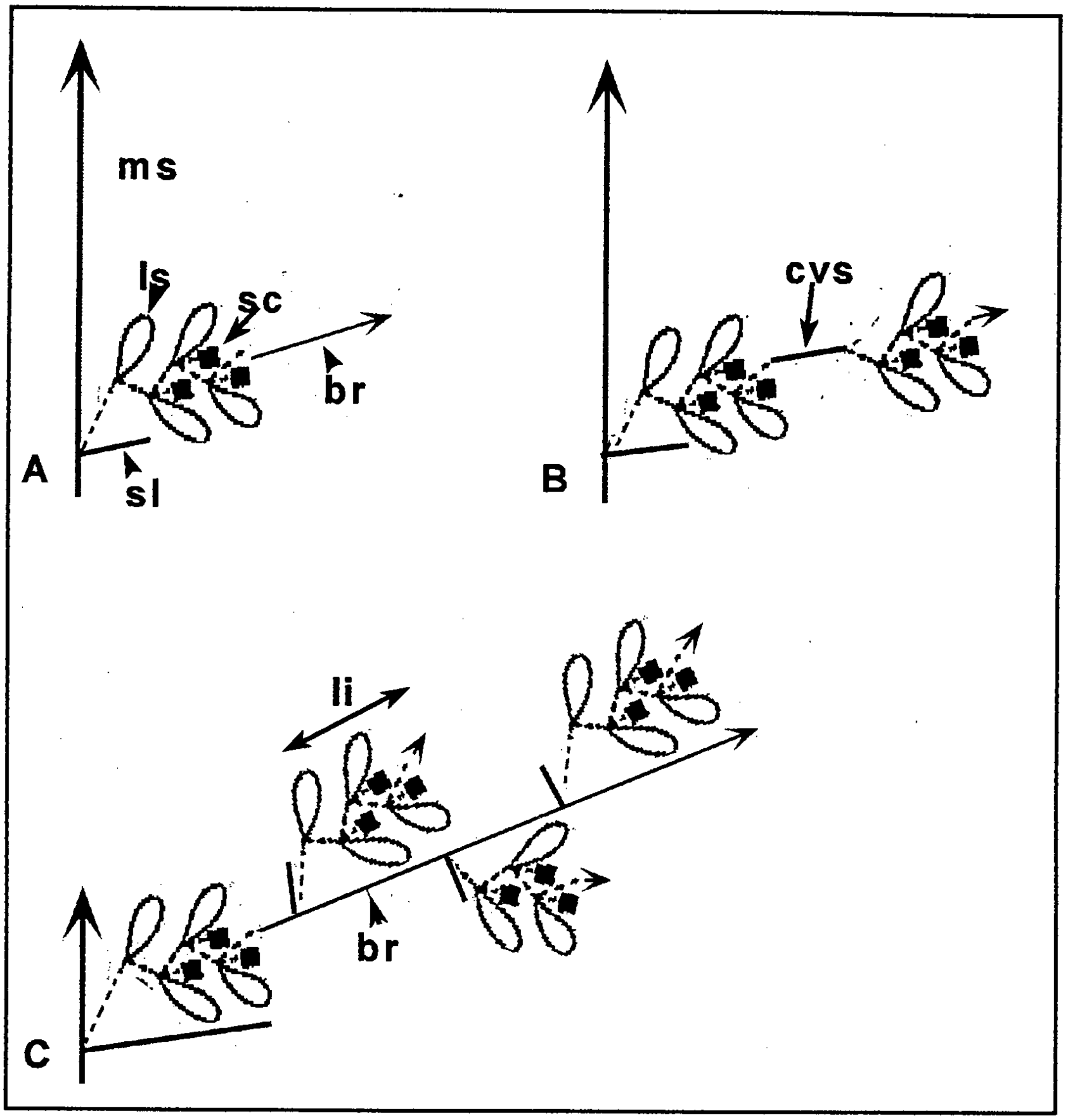

Fig. 5.4A-C. Longitudinal diagrams of inflorescences of *C. odorata* in different stages of development. **A**, compact mature inflorescence with apical branch; **B**, open inflorescence separated into two parts by a central vegetative short shoot; **C**, later developmental stage with three lateral inflorescences; ms, main stem; ls, leaf sheath subtending sub-cluster; sl, subtending leaf; sc, sub-cluster; br, branch; cvs, central vegetative short shoot; li, lateral inflorescence.

short shoot (ultimate flower-bearing disc) does not proliferate.

6. Sexuality of the plant:

With male and female flowers randomly mixed in the inflorescence, this is a monoecious plant.

7. Branching pattern:

Branches originate as the apical proliferation of inflorescences. Since inflorescences are generated continuously near the tops of vegetatively growing main stems, the occurrences of inflorescences and the subsequent development of branches are abundant. Both the zig-zagging of the main stems and the wide angle at which the branches meet the main stem, are determined by the crowding of the space between the subtending leaf and the main stem. The developing condensed inflorescences expand into this space, displacing the main stem and the branch.

6. ***Cliffortia arborea*** Marloth

For a considerable time, this species was the only known ‘tree’ in the genus. Marloth (1905) noted the height as occasionally up to 10 m .

Since it’s discovery in the mountains near Sutherland, further collections extended the distribution range of this species northwards to the Hantams Mountain near Calvinia and eastwards to the Nuweveld Mountains near Beaufort West.

In a fairly large and dense population on the Nuweveld Mountain escarpment, on terraces against rock ledges about 100 m away from the sheer cliffs, the growth form was that of upright trees up to 4 m tall, with main trunks to 15 cm in diameter and with reddish brown flaking bark. On the edge of the cliffs, the population was smaller and the growth form more stunted and compact. The taller plants in the first population, also produced mostly female cones while the stunted ones on the edge of the cliff, were almost totally covered in male flowers from just below the occasional apical female cones to the lowest branches brushing the ground.

On young plants flowering for the first time, the female cones appear as apical thickenings on the ends of main branches. It is on older plants that the female inflorescence cones are clearly seen to occur in series, from the older ones below to the one of the current season above, clasping proliferating main branches. Occasionally cones are also found on side branches originating from older cones lower down on main branches.

Female inflorescence:

A number of condensed lateral double racemes (homothetic dibotrya), are aggregated and spirally arranged on a condensed main axis, to form an oblong cone-like polytelic synflorescence (Figure 6. 2A: SN).

In the young (current season’s) cone, each dibotrys culminates in a coma of vegetative leaves forming a star-shaped rosette. Together, the rosettes cover the cone in a shroud of neatly arranged stars, from which the common name for this species viz. “Sterboom” (English: ‘Star Tree’) is derived.

On the main axis of the cone, trifoliolate primary cone leaves with broadened curved sheaths with or without pungent stipules, are spirally arranged (Figure 6.1B & 6.2B: pcl).

Each primary cone leaf subtends and surrounds a dibotrys (DB). A dibotrys consists of a number of co-florescences (CoF) on a secondary axis which is basally much condensed but apically proliferates into a vegetative shoot, bearing the star-like coma of vegetative leaves. The co-florescences (botrya)

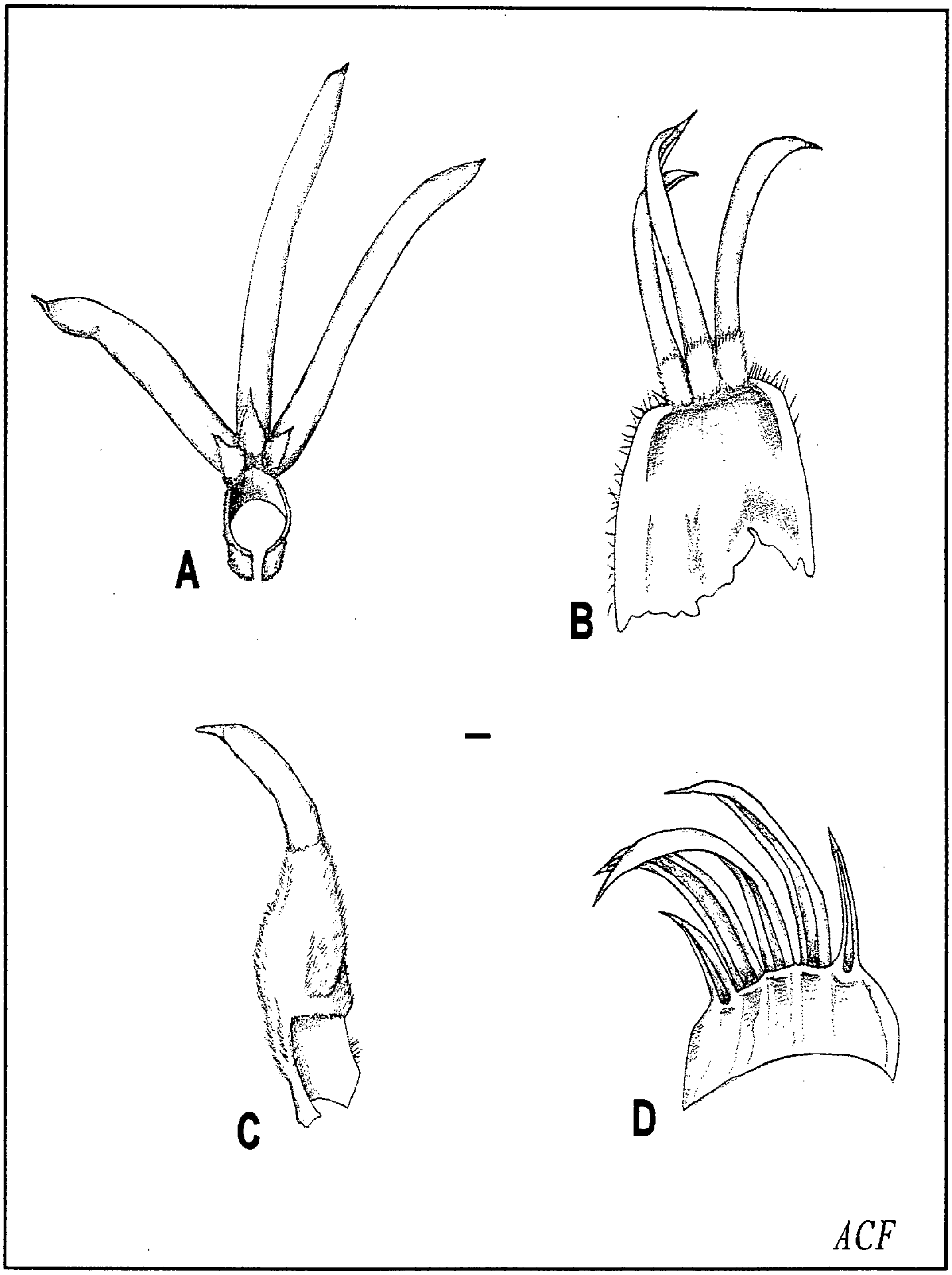

Fig. 6.1A-D Leaf types in ***Cliffortia arborea.*** **A,** vegetative leaf, adaxial view; **B,** primary cone leaf, a-stipulate type, adaxial view; **C,** secondary cone leaf, lateral/adaxial view; **D,** leaf from region directly below cone, abaxial view. All drawn from *Oliver* 10054 (NBG). Scale bar = 1 mm.

are arranged on the basal condensed part of the axis and surrounded by involucre-like groups of unifoliolate secondary cone leaves (scl), which form the firm part of the cone underneath the shroud of comas. The botrya (coflorescences) are highly condensed with the axes not more than a slightly raised flattened area bearing a number of tiny flowers in a capitulum-like arrangement. The flowers are largely hidden by the secondary cone leaves with not much more than the strap-shaped styles and stigmas showing (Figure 6.1C, 6.2B-D).

Older cones (of the previous season) proliferate apically into a short vegetative continuation of the main axis which will give rise to the following season's cone. Furthermore, the star-like comas of vegetative leaves marking the apices of the dibotrya, proliferate into vegetative side branches. These can bear female cones, male flowers or eventually thicken and continue the vegetative development of the plant (Figure 6.2A: VB).

Old cones are retained on main stems for a number of years but eventually disintegrate. This happens in stages. Firstly, after three or four years, abscission of the secondary cone leaves takes place at the top of the sheaths, leaving the woody bases on the main branches for several years. Eventually the clusters of secondary leaf bases get separated from each other, as the main branches bearing them undergo longitudinal growth and secondary thickening. By that time, the leaf bases will have been reduced to a few scattered scales on the main stem and will be hardly recognizable as the remains of the original cone.

Male inflorescence:

Male inflorescences are simple clusters of a few e-bracteate flowers in the axils of vegetative leaves on lateral branches. These are borne below the female cones but on the same main branches. (*Acocks* 18625; *Marloth* 9730; *Fellingham* 1625). Occasionally male flowers also occur on the thin side branches originating from older female cones (*Fellingham* 1625), but always occur lower down on the plant than the female inflorescences of the same season.

While distinctly monoecious, this species never have the male and female flowers occurring in the same inflorescence. Where male flowers do occur on the thin vegetative side branches of the occasional older female cones, as seen in *Fellingham* 1625, they are more than a year younger than these female cones and borne on vegetative shoots and not on the female cones themselves.

Summary:

1. The viability of apical buds:

On main stems and main branches the apical buds remain viable, proliferating to bear the next season's cone.

The apical buds of the dibotrya remain viable to give rise to the star-like comas that develop into the vegetative side shoots in the following season. Occasionally the development of side branches is aborted, probably due to harsh climatic conditions.

2. Position of flowers:

Due to the highly contracted nature of the flower-bearing parts, the stance of the flowers could not be defined as opposite or alternate.

3. Types of short shoots:

In the female cone three types of short shoots can be distinguished. The main axis of the cone is one, the main axis of the dibotrys the second and the flower-bearing capitulum-like structure, the third.

The male flowers, being clustered in little e-bracteate groups, share a contracted short shoot somewhat similar to, but smaller than that bearing female flowers.

4. Subtending leaves:

The female flowers themselves are largely e-bracteate through extreme modification and reduction of the ultimate co-florescences. There are however, primary cone leaves subtending and surrounding the dibotrya and secondary cone leaves subtending the co-florescences. Male flowers are e-bracteate.

5. Short shoots and long shoots:

Three types of short shoots occur in the female cone. The first order short shoot, constituting the main axis of the cone, proliferates to continue the linear growth of the main stem as a long shoot. The second order short shoot forms the axis of the dibotrys and gives rise to vegetative side (long) shoots on the female cone. Third order short shoots, the capitulum-like flower-bearing structures, do not proliferate. In none of these short shoots do the internodes lengthen.

Long shoots originate from first and second order short shoots and from vegetative branches. Male flowers are borne in small clusters, on highly modified and condensed short shoots, which in turn are borne in the axils of vegetative leaves on long shoots.

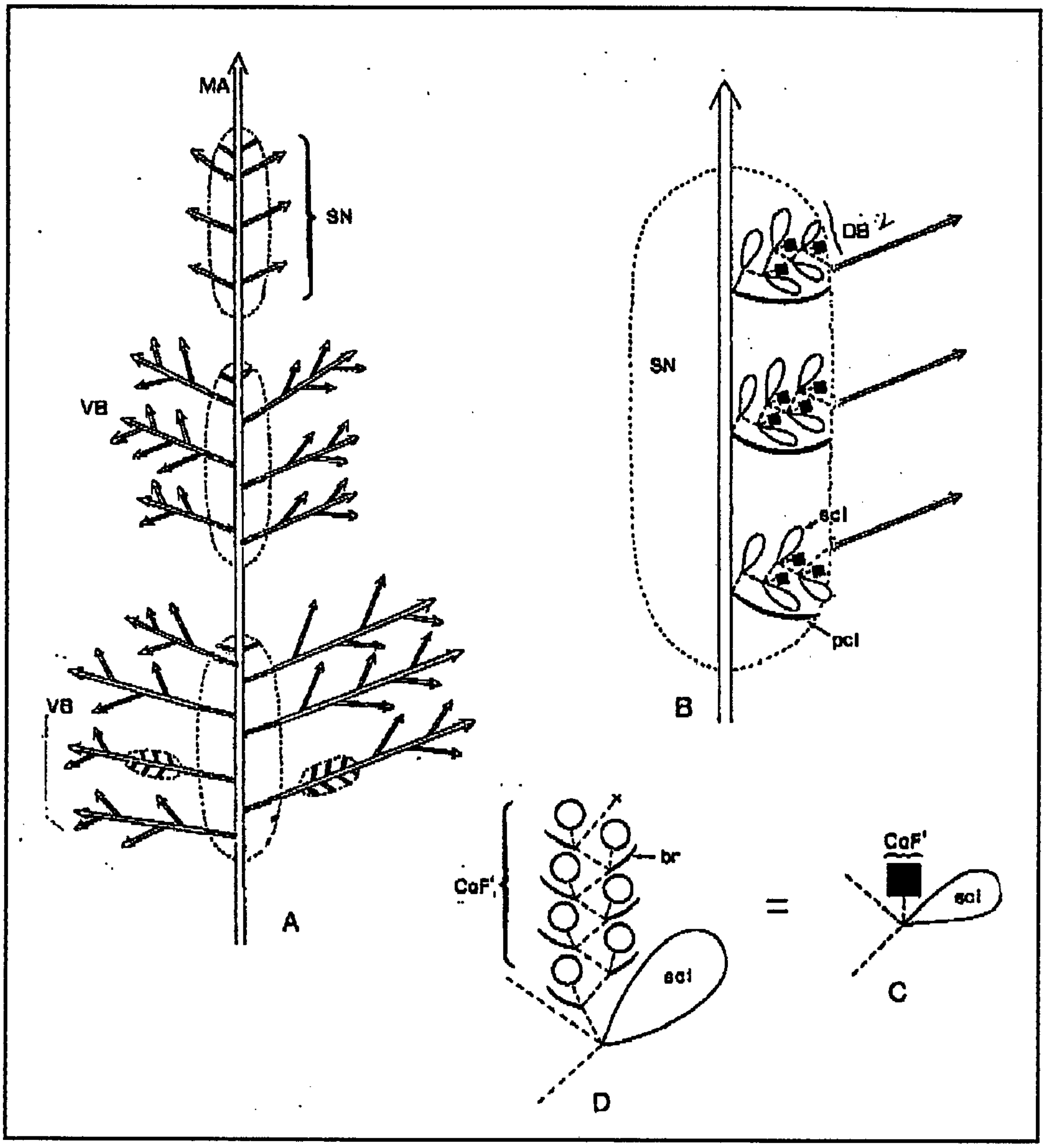

Fig. 6.2A - D. Longitudinal diagrams of inflorescences in *C. arborea*. **A**, three female cones on main branch and two on lateral branches; **B**, part of cone showing three dibotrya with vegetative branches; **C, D**, single botryum or co-florescence (solid square), expanded to show individual flowers (circles). MA, main stem; VB, vegetative secondary branch: SN, synfloresecense; DB, dibotryum; CoF, co-florescence or botryum; pcl, primary cone leaf; scl, secondary cone leaf; br, bract of single flower. Broken lines = axes of short shoots.

6. Sexuality of the plant:

Male and female inflorescences always occur on the same plant, which is, therefore, monoecious.

7. Branching pattern:

Linear growth of main branches is slowed down for the development of the female cone surrounding the stem, but continues normally again afterwards. Side shoots continue to develop on the cone once the formation of the second order short shoots is complete and proliferation of their apical buds occur. As a result of the contracted nature of the cone axis from which these side shoots originate, they are closer to each other than those on vegetative parts. They are also delayed in appearing as their basal parts are made up of the very short second order short shoots, forming the axes of the dibotrya. The main influence of the occurrence of female cones on vegetative branches is to slow down their linear growth temporarily, by the inhibition of the development of the internodes in the region that constitutes the inflorescence axes.

7. ***Cliffortia dichotoma*** Fellingham MS

This new species of *Cliffortia* section Arboreae, from near Nieuwoudtville, Namaqualand, is closely related to *C. arborea*.

It occurs on rocky ledges, on slight northern and southern slopes between two kloofs and beyond the southern one, on the Oorlogskloof escarpment, south of the Oorlogskloof Nature Reserve. The whole population is old and moribund, with part of every plant dead and dry. No seedlings have been found for at least 25 years.

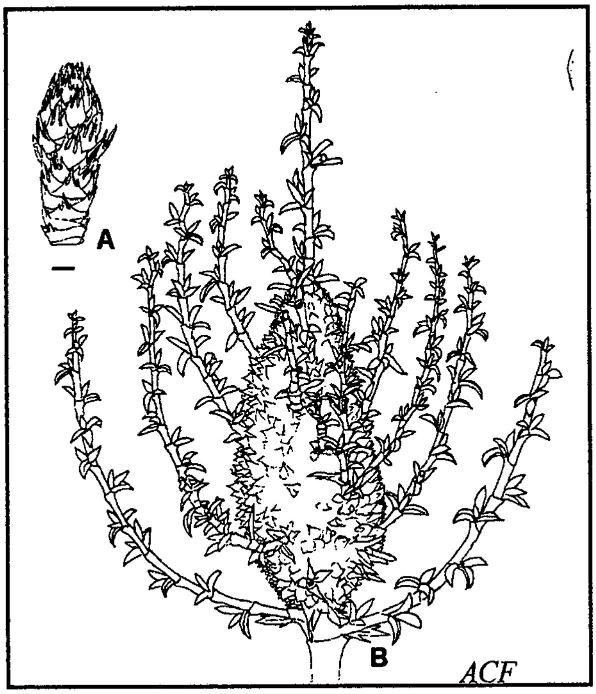

Fig. 7.1A & B, *Cliffortia dichotoma*. A, Apical swelling; **B**, female inflorescence cone. *Fellingham* 1684 (BOL, NBG). Scale bar = 1 mm.

The plants appear more tree-like than any other species in the genus and are up to 5 m tall. The main trunks are buttressed and therefore irregular in shape, up to 50 cm by 30 cm in cross section, and bare for the lower 50 cm. Branching is dichotomous from below a cone, with the new seasons cones at the tips of the new branches. This branching pattern results in a tree with a spreading canopy.

On my first visit to the site in September 1995, the trees bore two totally different structures. The one was a peculiar swelling covered in imbricate, hard, spiky, tridentate leaves with broad, amplexicaul sheaths, at the tips of some branches (Figure 7.1A). The second was recognizable as the female inflorescence cone, shrouded in numerous upwardly curving vegetative branchlets originating from the sides of the cone, plus one apical,

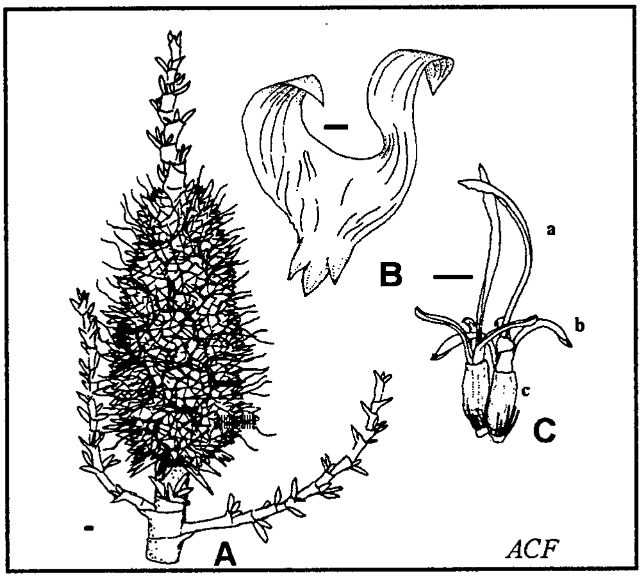

Fig.7.2A & B, *Cliffortia dichotoma*. A, young female cone; **B**, primary cone leaf; **C**, female flowers. a, style; b, calyx lobe; c, ovary. *Fellingham* 1689 (BOL, NBG). Scale bars = 1 mm.

straight and slightly more robust, branchlet. The two branches just below the cone were close together and clearly more robust than the ones lower down (Figure 7.1B).

My second visit, in November of the same year, yielded a different perspective. The apical swellings of Springtime, were then fully developed young female cones with numerous circles of long, maroon, strap-shaped stigmas marking rosettes of conical, hairy and pointed modified leaves, some with central raised areas punctuated by 'stars' of about 5 vegetative leaves. The two lateral branches directly below the cone were by then already showing signs of thickening and curving upwards in preparation for the production of the following season's pair of apical cones (Figure 7.2A). Some of the previously 'shrouded' cones were also becoming bare, even losing the apical branchlets.

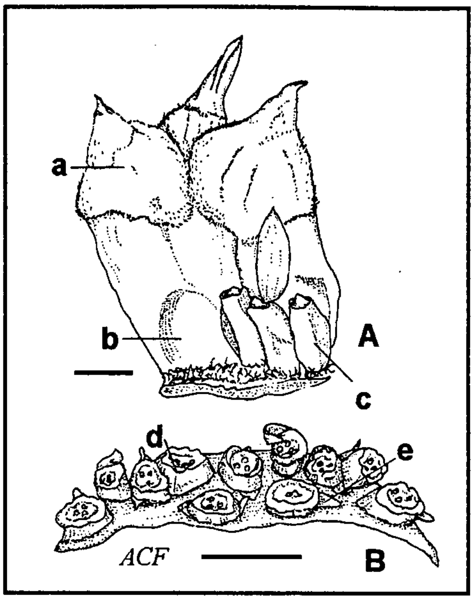

Fig. 7.3A & B, *Cliffortia dichotoma.* **A**, secondary leaf bearing botrys in axil; **B**, capitulum-like botrys. a, leaf blade; b, cavity in leaf sheath; c, fruit; d, pedicel; e, modified bract. *Fellingham*1684 (BOL, NBG) Scale bars = 1 mm.

During the particularly dry season of 1997, which followed the extremely wet season of the year before, an occasional unusual arrangement of cones was observed. Instead of the two side branches from below the current season's cone elongating in preparation the production of the terminal cones in the next season, they were stunted and gave rise to a cone each immediately below the current cone, resulting in a cluster of three cones.

Female inflorescence:

A number of lateral condensed double racemes (homothetic dibotrya) (DB), each consisting of a few sessile capitulum-like co-florescences (botrya) (CoF), are aggregated and spirally arranged on a condensed main axis, to form an oblong cone-like polytelic synflorescence on the end of a main branch, originating as one of a pair from below a cone of the previous season (Figure 7.2A & 7.5A-D). Each dibotrys is subtended by a primary cone leaf (pcl) with a grossly extended sheath segregating the individual dibotrya from each other, and a tridentate, often stipulate, woody blade just emerging between the involucres of secondary cone leaves (Figure 7.2B & 7.5B). The secondary cone leaves have thickened woody sheaths without stipules and swollen trifoliolate blades, with the leaflets of each leaf arranged in triangles(Figure 7.3A & 7.5B, C& D: scl). Both the primary and secondary cone leaves differ from the ordinary vegetative leaves which are small, unifoliolate and ligulate in shape (Figure 7.4A). Each secondary cone leaf subtends a capitulum-like botrys bearing up to 12 flowers on minute pedicels, subtended by greatly modified bracts (Figure 7.3B). The flowers, each with three or four calyx lobes, are totally hidden amongst the secondary cone leaves with only their ligulate styles protruding. (Figure 7.2A & C) The fully developed fruits are irregularly angular and closely packed in the concavity in the adaxial side of the sheath of the secondary cone leaf which subtends the capitulum-like flower-bearing structure, the coflorescence (Figure 7.3A & B).

In the mature young cone in which proliferation of the apical bud has already given rise to a conspicuous vegetative continuation of the main stem, spirally arranged circles of long maroon stigmas - each circle with a tridentate, woody, primary leaf below it - demarcate the double racemes (dibotrya) (Figure 7.2A).

In the slightly more mature cone with withered stigmas, the centres of these circles are raised as the second order axes proliferate, and each circle becomes crowned with a star-like arrangement of vegetative leaves. As the second order axes elongate in the more mature cone, the 'stars' are replaced by a shroud of vegetative side shoots (Figure 7.1B). The appearance of the 'stars' that are to develop into the shroud of side shoots, seems to coincide with fertilization, as at that point the styles begin to dry and shrivel. As much older cones once again become bare, shedding even the apical proliferation of the main stem, it seems that the shrouds of shoots are in place during the development of the fruits, which is the rest of the current season and the following one.

Male inflorescence:

Very shortly pedicellate male flowers with much reduced bracteoles, 4 calyx lobes and 4 stamens, occur singly or in small groups, in the axils of ordinary vegetative leaves on branchlets lower down on the main branches bearing the female cones (Figure 7.4 A & B).

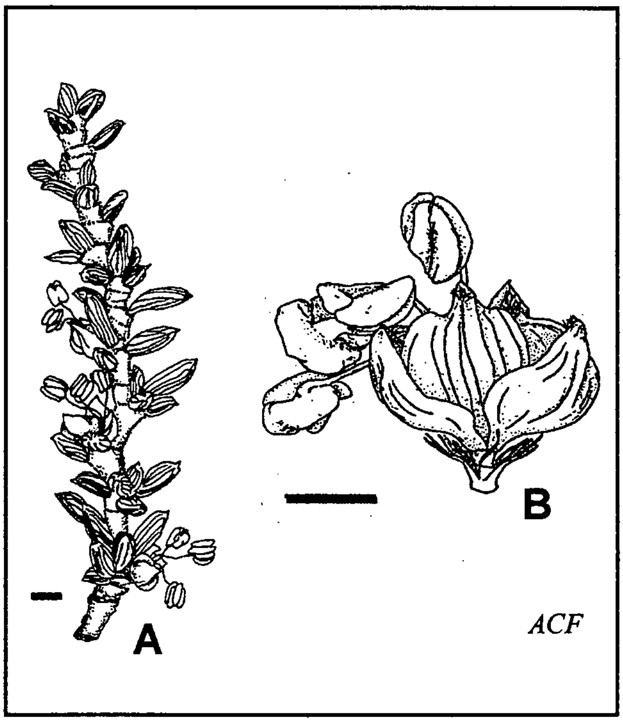

Fig. 7.4. ***Cliffortia dichotoma.*** **A**, vegetative branchlet with male flowers; **B**, male flower. *Fellingham* 1689 (BOL, NBG) Scale bars = 1 mm.

Summary:

1. The viability of apical buds:

The apical bud of the main stem, which is also the main axis of the inflorescence, remains viable till the apical long shoot is fully developed, which is at the time of flowering.

The apical buds of the dibotrya remain viable till the vegetative side shoots are fully developed, which is soon after fertilization has taken place.

The only apical buds that remain viable long enough to ensure linear growth, are those on the two side shoots below the female cone. These give rise to the robust dichotomous branches on the tips of which the new season's cones will be borne.

2. Position of the flowers:

Due to the highly condensed nature of the co-florescences, the stance of the flowers could not be determined.

3. Types of short shoots:

In the female cone three types of short shoots can be distinguished. The main axis of the cone is one, the main axis of the dibotrys is the second and the flower-bearing capitulum-like structure, the third.

The male flowers, being clustered in small e-bracteate groups, can be seen as sharing a condensed short shoot, similar to, but smaller than the female flower-bearing one.

4. Subtending leaves:

The female flowers are subtended by diminutive bracts, while the male flowers are e-bracteate. There are however, different structures subtending partial inflorescences, viz. primary cone leaves subtending and surrounding the dibotrya and secondary cone leaves subtending the co-florescences.

5. Short shoots and long shoots:

Of the three types of short shoots in the female cone, only two give rise to long shoots viz. the main axis of the cone and the main axes of the dibotrya. The third, the capitulum-like structures of the co-florescences, remain highly modified short shoots. The short shoot bearing the male flowers is similar but smaller than this capitululm-like structure.

Permanent vegetative growth depends entirely on the pair of vegetative branches, originating from the main stem.

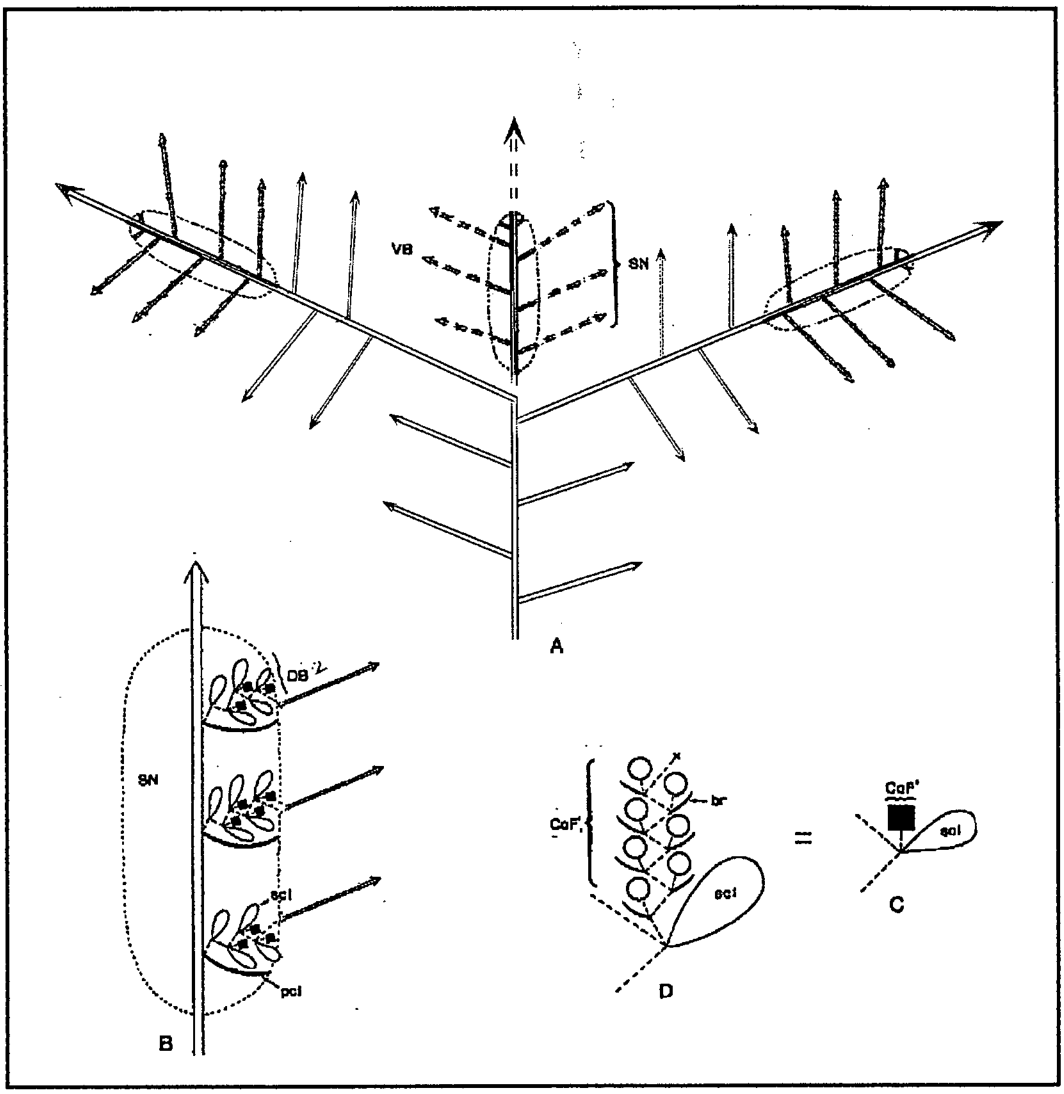

Fig. 7.5A-D, Longitudinal diagrams of inflorescences in *C. dichotoma*. **A**, three female cones on dichotomous branches, the central one of a previous season, having already lost it's apical and lateral branches; **B**, part of a cone showing three dibotrya with vegetative branches; **C, D,** single botryum or co-florescence (solid square), expanded to show individual flowers (open circles).VB, vegetative secondary branches; SN, synflorescence; DB, dibotryum; CoF, co-florescence or botryum; pcl, primary cone leaf; scl, secondary cone leaf; br, bract of single flower. Broken lines = axes of short shoots.

6. Sexuality of the plant:

The plant is monoecious with male and female inflorescences always on the same plant.

7. Branching pattern:

The abortion of the apical shoot and the side shoots of the female cone, leaving the burden of vegetative growth on the two vegetative branches at the base of the inflorescence, produces a peculiar dichotomous branching pattern.

*8. **Cliffortia conifera*** E.G.H. Oliv. & Fellingham

The only known population of this species is a very small one on an east facing cliff edge, on the Anysberg. The group of tree-like shrubs up to 4 m tall and with the main trunks up to 150 mm in diameter, resemble conifers in their upright growth form, as well as in their cone-like inflorescences, each terminally on a short lateral branchlet. These cone-bearing branchlets occur in groups of up to 10 in subterminal zones on main branches; rarely on secondary branches. Older branches have several zones of cones interspersed with vegetative regions consisting of well developed leaf-bearing lateral branches.

The plants are so unlike any known *Cliffortia,* and the cones unlike any inflorescence in the genus that, when first encountered by Mariana van Wyk on a collecting trip of members of staff of the then Stellenbosch Herbarium in October 1982, the cones were taken to be galls on totally unknown plants. It was only when Pauline Fairall (Bond) of the Compton Herbarium (NBG) opened a 'gall' and found minute female flowers in it, that it became clear that the cone was indeed a female inflorescence and the plant a possible new species of *Cliffortia* (Figure 8.1A).

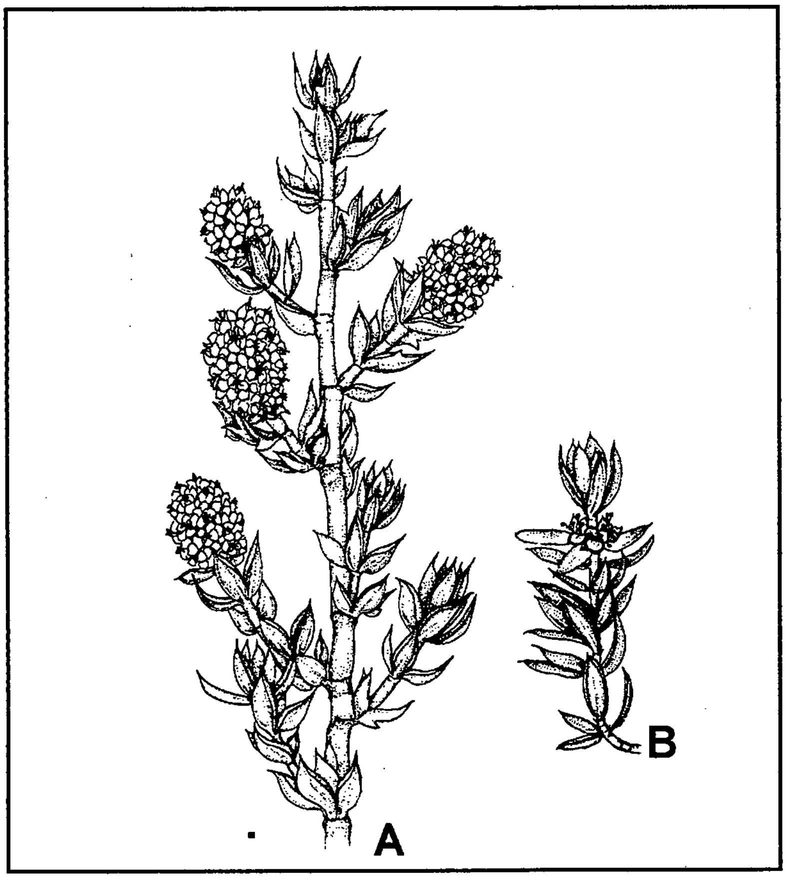

Fig. 8.1 A & B *Cliffortia conifera:* **A**, branch bearing female cones; **B**, branchlet bearing male flowers. Drawn by Inge Oliver from *Oliver* 10055 (NBG). Scale bar = 1 mm.

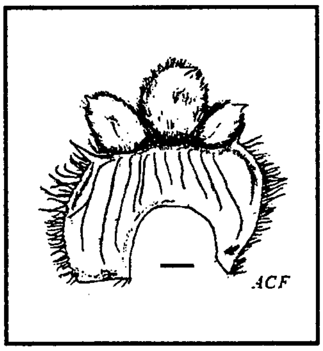

Fig. 8.2 ***Cliffortia conifera:*** primary cone leaf. *Oliver* 10055 (NBG). Scale bar = 1 mm.

Female inflorescence:

The obovoid or occasionally spheroid cone consists of many condensed double racemes (homothetic dibotrya) aggregated on a shortened main axis, which is in fact, the condensed end of a lateral branchlet. The cone is devoid of proliferating shoots, either from the ends of the double racemes or the apex of the cone (Figures 8.1A & 8.4A & B).

The cone can be seen as a polytelic synflorescence composed of numerous (up to 50), condensed, sessile, racemes (botrya), the co-florescences, grouped together in highly condensed double racemes (dibotrya). The co-florescences resemble capitula with up to 16 flowers all arising at the same level from the truncated end of the very short, 3rd order, florescence axis. The flowers are interspersed with long erect hairs from which the variously modified and reduced bracts just emerge. Except for the protruding stigmas and occasionally the small calyx lobes, the flowers (and eventualy the fruit) are concealed by the bulbous secondary cone leaves on the 2nd order cone axes, which are involucrally arranged and form the matrix of the cone. The secondary cone leaves are unifoliolate, lack both stipules and sheaths but have a demarcation between the upper bulbous part with velvety indumentum, and the basal flattened glabrous part (Figure 8.3, 8.4B: scl). The primary cone leaves originate on the main cone axis, subtend the lateral second order dibotrya and are also concealed by the secondary cone leaves. The primary cone leaves differ from the secondary cone leaves in the having extended leaf sheaths with stipules and, being uni- or trifoliolate. (Figure 8.2, 8.4: pcl) Both the primary and secondary cone leaves differ from the ordinary vegetative leaves which are trifoliolate, the leaflets flat with rolled edges and plain to tri-dentate and the sheath amplexicaul and stipulate (Figure 8.1A & B).

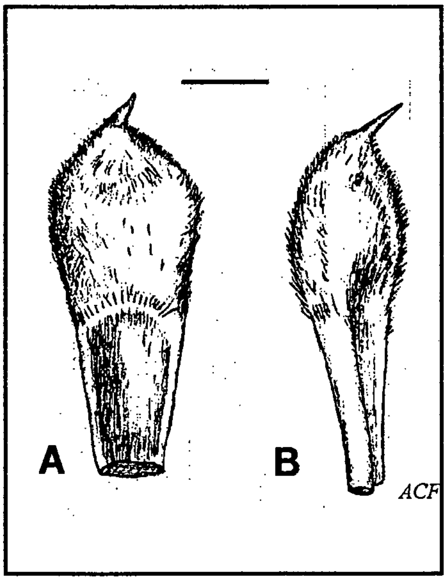

Fig. 8.3 A & B, ***Cliffortia conifera:*** secondary cone leaves; **A,** adaxial view; **B,** lateral view. *Oliver* 10055 (NBG). Scale bar = 1 mm.

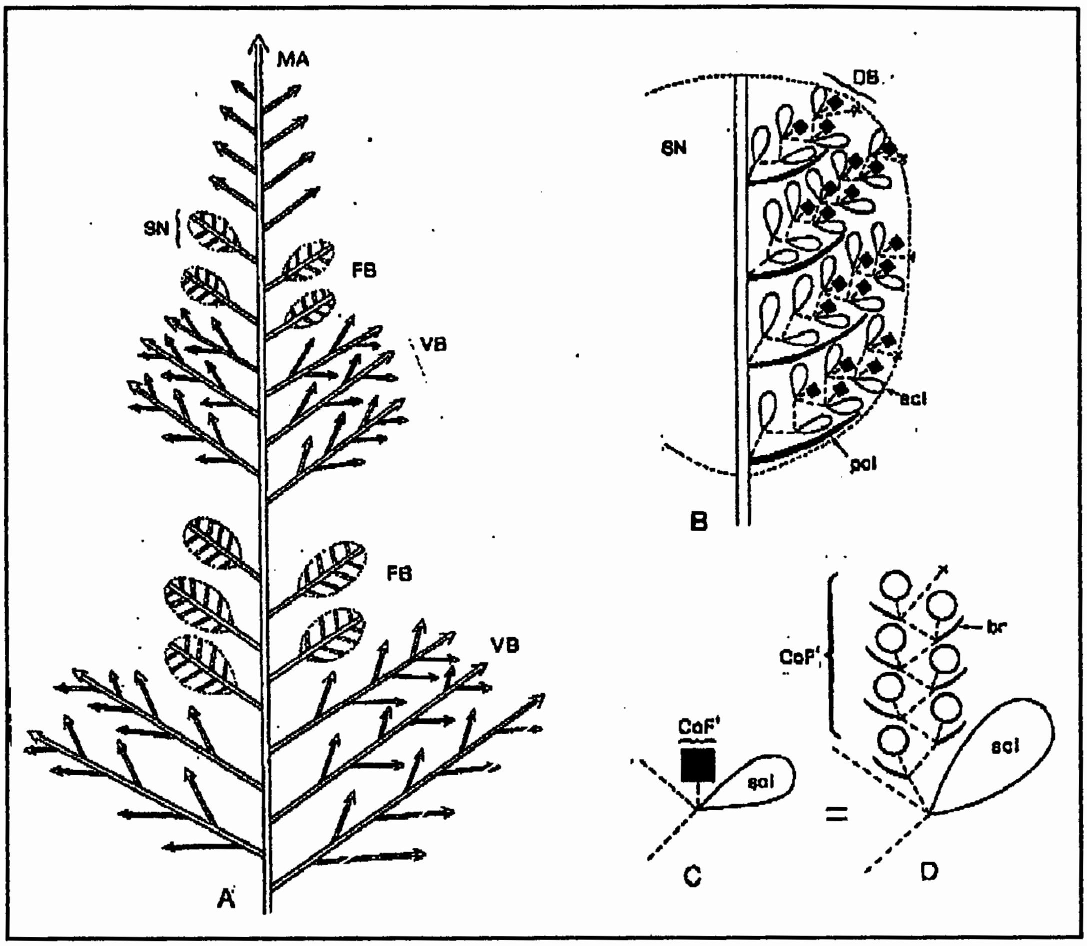

Fig. 8.4A-D, Longitudinal diagrams of inflorescences in *C. conifera.* **A**, main branch with two cone-bearing zones. **B**, part of female cone showing four dibotrya. **C, D**, single botryum or co-florescence, (solid square) expanded to show individual flowers (circles). MA, main stem; FB, flowering secondary branches; VB, vegetative secondary branches; SN, synflorescence; DB, dibotryum, CoF', co-florescence or botryum; pcl, primary cone leaf; scl, secondary cone leaf; br, bract of single flower. Broken lines = axes of short shoots.

Male inflorescence:

The male inflorescence is a much simpler structure, consisting of a cluster of 3 or 4, occasionally 5 flowers, on a highly reduced short shoot, in the axil of a sub-apical vegetative leaf, on lower lateral branches, well below zones of female cones. (Figure 8.1B)

Summary:

1. The viability of apical buds:

The apical bud of the main axis of the inflorescence, loses its viability as soon as the axis is fully formed, as do the apical buds of the constituent dibotrya.

2. Position of the flowers:

This could not be determined due to the specialized nature of the highly condensed co-florescences.

3. Types of short shoots:

Permanently highly condensed short shoots occur in three positions in the female cone, viz. the main axis of the cone, the main axis of a dibotrys and the capitulum-like flower-bearing structure.

The clusters of male flowers originate on condensed short shoots, similar to the capitulum-like structures of the female inflorescence.

4. Subtending leaves:

The female flowers are subtended by diminutive bracts and the male flowers are e-bracteate. Partial florescences are subtended by primary or secondary cone leaves as the case may be.

5. Short shoots and long shoots:

None of the three types of short shoots in the female cone lengthen or proliferate, therefore, no long shoots develop out of short shoots.

6. Sexuality of the plant:

Male and female inflorescences on the same plant renders it monoecious.

7. Branching pattern:

With the non-proliferating female cones occurring at the ends of short side branches, linear growth of the main stem is left uninterrupted, resulting in a upright, sparsely branched growth form.

Chapter 4: Discussion

When Weimarck (1934) recorded the mode of flower-bearing in the majority of *Cliffortia* species as that of 'flowers borne solitary in the axils of ordinary vegetative leaves', he reported on evidence gained at superficial examination. What appears to be a single flower directly in the axil of a leaf, is in fact, a single-flowered inflorescence. This consists of a short shoot with a single internode and a single node on which the single, lateral, bracteate or often e-bracteate flower is borne. Unlike the flexible condition demonstrated by Briggs and Johnson (1979) in the Myrtaceae, where a shoot may terminate either in a flower or a (vegetative) bud, in *Cliffortia* the shoot always terminates in a vegetative bud, and the flower always occurs laterally on the shoot.

The existence of this short shoot and the lateral stance of the flowers borne on it, are clearly demonstrated in instances where the originally single flower on a developing inflorescence, is joined by subsequent flowers and the initially minute short shoot bearing these flowers, enlarges and eventually proliferates into a long shoot. This is clearly seen in the secondary short shoots in *C. heterophylla* which originate as minute short shoots bearing single female flowers. The initially single-flowered inflorescence developing further into a complex and condensed multi-flowered inflorescence, once the initial flowered had matured, as found in *C. crenata,* is another illustration. (Figures 4.2 , 2.1B &2.2C).

In *C. nivenioides* where no subsequent flowers develop, the position of the single flower can be deduced from the fact that the leaf axil, occupied during the fertile stage by this flower, will be occupied by a vegetative short shoot in the vegetative stage. This could only ensue if the flower had been positioned laterally on the first (basal) node of a minute, basic, single-flowered short shoot inflorescence. The apical bud of this minute inflorescence would then proliferate into the vegetative shoot during the vegetative stage. In order to interpret this structure correctly, the fact that the vegetative shoot, bearing the basic single-flowered inflorescences, is a short shoot and not a long shoot as in the majority of species, must be kept in mind. The imbricate arrangement of the vegetative leaves subtending these single-flowered inflorescences, creates the illusion that the short shoot is a single inflorescence with vegetative leaves, each subtending a single flower. However, the subtending leaves, though imbricate, should not be interpreted as bracts, nor the vegetative short shoot as a multi-flowered fertile short shoot. What appears to be a fertile short shoot, differing from the norm by its vegetative subtending leaves, is in fact a clustering of basic, single-flowered inflorescences, on a vegetative short shoot instead of on the usual long shoot.

The distinction between a single flower and a single-flowered inflorescence lies in the fact that an inflorescence is subtended by an ordinary vegetative leaf while the individual flower is bracteate, or rarely e-bracteate. The basis for this distinction lies in the shift of the interpretation of the position of the flower from terminal with its pedicel originating directly in the axil of the subtending vegetative leaf, to lateral on a minute short shoot in the axil of the subtending vegetative leaf. Thus, in its simplest form, as it occurs in this species, the inflorescence is single-flowered with the apical bud dormant for the rest of the fertile stage. Only at the onset of the vegetative stage will it proliferate.(Figure1.2A - C).

In some species this simple form can exist in conjunction with, or develop into, a more advanced one with multiple internodes, nodes and flowers. The development of the multi-flowered inflorescence out of the initially single-flowered one happens after the first flower has matured. When this is the case, it is usually accompanied by sexual segregation of the flowers with the female flowers on the proximal short shoot and the male flowers on the basal nodes of the distal long shoot, arising as the apical proliferation of the short shoot. In this instance each male flower is borne on the simplest form of the inflorescence as described above - a short shoot with a single internode, a single node and a single e-bracteate flower - borne in the axil of a vegetative leaf on the proximal long shoot. What thus appears to be a simple inflorescence with a proximal female flower-bearing short shoot, continuing into the distal male flower-bearing long shoot in a linear fashion, is in fact a more complex system. The distal long shoot forms the axis of a system of single-flowered short shoot inflorescences, bearing the male flowers, before proliferating further into a purely vegetative long shoot. Thus the proximal multi-flowered female short shoot proliferates into a system of secondary minute short shoots, each bearing a single male flower. This is clearly seen in the development of the secondary short shoots in *C. heterophylla* (Figure 4.2).

The multi-flowered inflorescence can also develop gradually with its flowers in sequential stages of maturity from the proximal to the distal, all originating from the nodes of the short shoot and with the sexes mixed. In this case the apical proliferation shoot is a purely vegetative shoot and develops at the onset of the vegetative stage. Here the inflorescence consists of a single, multi-flowered, sexually integrated, short shoot and not a system of short shoots as in the previous case with segregated sexes.

When the axis of the short shoot inflorescence is condensed even further, it can become a flattened disc, borne in the axil of a vegetative leaf on a main stem, or an irregular flower-bearing platform, borne in the axil of a bract on a secondary inflorescence axis. This disc occurs thus either as the primary non flower-bearing short shoot or the secondary (ultimate) flower-bearing disc or platform in a system consisting of highly condensed primary and secondary short shoots. It can also occur in a single inflorescence as both the primary short shoot which is sessile in the axil of a vegetative leaf on a main stem, and the secondary flower-bearing disc, which is stalked and subtended by a bract.

In inflorescences consisting of a system of short shoots of primary and secondary or primary, secondary and tertiary short shoots, it is always only the ultimate short shoots that are dedicated to flower-bearing, to the extent that the viability of their apical buds is lost. The apical buds of the lower order short shoots, forming the matrix of the inflorescence, however, retain their viability. These are the short shoots that can undergo one of two changes, or a combination of these two, at the onset of the vegetative stage or, in some instances, during the development of the inflorescence. The changes to the short shoot are the lengthening of the internodes rendering it a long shoot, the proliferation of the apical bud into an apical long shoot, or both lengthening and proliferation. With the lengthening of the internodes, it becomes a long shoot without leaving a trace of the original short shoot. With the addition of apical proliferation to the lengthened shoot, the ensuing long shoot would gain greatly in longitudinal growth. It is only in the case of apical proliferation without any lengthening of the internodes, that the original short shoot can still be discerned. It is this inherent morphological plasticity of the matrix of the inflorescence that renders it capable of contributing to the vegetative growth both in substance and pattern.

The basic single-flowered inflorescence occurs in *C. nivenioides, C. crenata, C. heterophylla* and *C. odorata*.

In *C. nivenioides* the mature inflorescences remain small single-flowered structures. Several of these are borne closely together in the axils of ordinary vegetative leaves on a vegetative shoot which, in this case, is a short shoot and not a long shoot as in the majority of species. In two ways does this vegetative short shoot behave like an inflorescence viz. in the eventual lengthening of its internodes and the proliferation of its apical bud to give rise to a vegetative short shoot, after the maturing of the flowers. In contrast, the single-flowered, single-internoded inflorescence by its very nature, cannot undergo lengthening. It does however, proliferate and here again the outcome is not a long shoot but a short shoot. What appears to be a multi-flowered short shoot with its flowers subtended by ordinary vegetative leaves, is in fact a system of short shoots, the ultimate ones being of the basic single-flowered type aggregated onto a short shoot axis.

In this species this vegetative short shoot is the only short shoot element that lengthens as the vegetative stage is entered. Vegetative growth depends on this lengthening of the axis of the vegetative short shoot plus the short shoots arising from the apical proliferation of the single-flowered inflorescences. Of the resultant short shoots, only the apical one and a few laterals just below the apex, retain the viability of their apical buds and are designated to bear the single-flowered inflorescences of the following fertile stage. The rest remain vegetative short shoots and do not contribute any further to the vegetative growth. This results in an exceptional preponderance of short shoots in the vegetative structure of this species (Figure 1.2A - E).

In *C. crenata* the inflorescence originates as a single-flowered one which develops into the multi-flowered, sexually segregated inflorescence, after the maturing of the initial female flower. The inflorescence thus consists of a proximal female short shoot and a distal long shoot bearing the single-flowered male inflorescences in the axils of its vegetative leaves. The whole system is subtended by an ordinary vegetative leaf on a main stem. (Figure 2.1A - H, 2.2C).

In *C. heterophylla* the origin and development of the inflorescence follows the same pattern as for *C. crenata,* with the important difference that the system is subtended by a primary bract on a primary short shoot, rendering it a secondary inflorescence axis in a more complex inflorescence. (Figure 4.2).

The single-flowered inflorescence in *C. odorata* very soon gives way to the highly condensed primary sessile disc, bearing the secondary stalked discs which are the ultimate flower-bearing structures. That the initial flower should mature before further development takes place in this complex system, seems strange. The transition from the single- to the multi-flowered condition can be seen on examination of the space between the mature flower of the single-flowered inflorescence, and its bracts, which contains immature flower clusters on a flattened, condensed axis. (Figure 5.1A & B).

A typical patently multi-flowered, bracteate, short shoot inflorescence with proximal permanent short shoot and eventual vegetative proliferation, as described above, is found in *C. ruscifolia.* The difference in the vegetative leaves on the main stem, subtending the inflorescence, and the bracts subtending the individual flowers, is obvious in this species, as is the permanent character of the short shoot axis. (Figure 3.1N & 3.2: iz,riz).

C. odorata, C. arborea, C. dichotoma and *C. conifera* represent the most complex of inflorescences with the ultimate flower-bearing discs or platforms dedicated to flower-bearing, having lost the viability of their apical buds. In *C. odorata* with its system of primary and secondary short shoots, the primary short shoot also assumes the form of a disc but is not flower-bearing and retains its viable apical bud. The proliferation of this gives rise to a lateral vegetative branch. The remaining three species represent permanent short shoots of three orders with again, just the ultimate short shoot dedicated to flower-bearing. Proliferation of primary and secondary short shoots takes place in *C. arborea* and *C. dichotoma,* giving rise to long shoots in both instances. However, it is in *C. arborea* only that these long shoots make a permanent contribution to the vegetative structure of the plant. In *C. dichotoma* the long shoots from both primary and secondary origin, are deciduous, being shed at about the time when the seeds mature. The highly modified cone in *C. conifera* has lost the viability of the apical buds of all three orders of its short shoots and therefore cannot contribute to the vegetative structure of the plant. The cone as a whole and not just the ultimate flower-bearing short shoot, has thus become dedicated to flower-bearing. (Figures 5.4A, 6.2A - D, 7.1B, 7.5A -D, 8.1A &8.4A -D).

The peculiar plasticity of the inflorescence is the result of the retention of the viability of the apical bud of one or more short shoots in the inflorescence, combined with the ability of the short internodes of the short shoot(s) to lengthen, generally at the onset of the vegetative stage but in some species, also during the development of the inflorescence. The parts of the inflorescence that do not contribute in this way, are the dedicated flower-bearing structures and those short shoot axes, the apical buds of which had lost their viability. The dedicated flower-bearing structures are the sub-clusters or co-florescences or capitulum-like botrya of the complex inflorescences of *C. odorata, C. arborea, C. dichotoma* and *C. conifera.* Short shoot axes without viable apical buds are those constituting the primary and secondary cone axes in *C. conifera.* These short shoots are thus incapable of any contribution to the vegetative structure of the plant. This renders the cones discreet modified side branches. (Figures 5.4A, 6.2B - D, 7.3A & B, 7.5B -D, 8.1A, 8.4A - D).

Plasticity resulting from a combination of apical proliferation and lengthening of the internodes, both of these changes taking place during the development of the inflorescence, is clearly seen in *C. heterophylla.* Here it is not only responsible for considerable vegetative change and growth but also brings about a sex change, from overtly female in the young inflorescence, through a bi-sexual stage to an overtly male stage (Figure 4.2). A similar sex change by segregation of the sexes in time, occurs in *C. crenata,* with the female flowers on the older short shoot portion and the male flowers on the proximal portion of the long shoot proliferation of the short shoot (Figure 2.2C). In *C. ruscifolia* too, the female flowers are usually lower in the short shoot inflorescence, and therefore older than the males (Figure 3.1A & N, and 3.2A). In *C. nivenioides* a segregation of the sexes exists in that the males occure lower down and are therefore, older (Figure1.2B). The segregation of the sexes in the species with female cones viz. *C. arborea, C. dichotoma* and *C. conifera,* is in location on the plant, with the male clusters lower down on the same branches as the apical female cones, seemingly flowering at the same time, thus not exhibiting any sex change. In contrast, the inflorescence in *C. odorata,* though highly condensed and modified, shows a surprising lack of segregation of the sexes in either time or space.

Furthermore, this phenomenon of morphological plasticity results in the integration of the matrix of the inflorescence into the vegetative part of the plant, with considerable influence on its branching pattern. The degree of involvement of the various orders of short shoots in the producing of long shoots and the abundance of inflorescences present, are the main determining factors here.

Thus, a sparsely branched lanky growth form is produced where flower-bearing is limited to a few apical vegetative short shoots. These are the only short shoots that eventually develop into long shoots (vegetative branches) by the lengthening of their internodes. This is the case in *C. nivenioides* (Figure1.2C - E).

By contrast, the rich and random branching pattern in *C. ruscifolia* originates from its numerous inflorescences. Most of these proliferate into vegetative long shoots (Figure 3.2D).

A sparse and virgate branching pattern results from the small percentage of inflorescences, all near the apex of the main stem, that proliferate. This is seen in *C. crenata* (Figure 2.2C: Ish).

The monopodial branching in *C. odorata* is the result of proliferation of the primary short shoots of numerous axillary inflorescences on main stems, which themselves grow vegetatively only (Figure 5.4A). The monopodial branching of *C. heterophylla,* however, is the result of a combination of two factors. The fast growing main stem gains from the lengthening of the primary short shoot of the apical inflorescence as well as the eventual apical proliferation. The limited linear increase in the lateral branches, originating from the proliferation of the second order short shoots, enhances this effect (Figure 4.2: dl). Similarly, in the young plant of *C. arborea,* the monopodial branching is regulated by the proliferation of the first order short shoot which is also the main stem of the plant. As the plant ages and side branches become involved in flower-bearing, the branching pattern is obscured (Figure 6.2A ; MA & VB).

A peculiar involvement of the position of the inflorescence determining the branching pattern is found in *C. dichotoma.* With the abortion of all initial proliferation shoots, two vegetative branches, close to each other and just below the terminal inflorescence, take over the function of continuing linear growth. These develop into a pair of thick main branches, one on each side of the central apical inflorescence. This results in the dichotomous branching pattern, unique in the genus (Figure 7.2A, 7.5A)

It is only in *C. conifera,* the species that exhibits no morphological plasticity of the inflorescence, that there is no effect of the inflorescence on the branching pattern, other than that a zone of branches are dedicated exclusively to the bearing of the female cones. In this aspect, it approaches the condition in the gymnosperms (Figure 8.1A, 8.4A).

The discovery of sex change or sequential hermaphroditism of the individual, sheds new light on plant sexuality. The condition in *C. heterophylla* clearly demonstrates a sex change of the individual over time. The individual always starts out as overtly female, then becomes bi-sexual and ends up as an overtly male. A single field observation of this plant during the first developmental stage, would have led to the conclusion that it is a female plant, where as, if the plant was observed in the third stage, it would have been labeled male. The bi-sexual individuals would be seen as anomalous and the species erroneously taken to be dioecious. Without careful and repeated field studies on a plant community, this phenomenon of morphological plasticity with its effect on the branching pattern as well as the sex of the individual, would have gone unnoticed. Though not as dramatic as in this species, a shift in preponderance of one or the other sex over time, does occur in *C. nivenioides, C. ruscifolia* and *C. crenata.* While no observable sex change occurs in those species with highly condensed and modified female cones, the sexes are segregated into male and female inflorescences. The female cones are borne near the tops of the main branches and the male flower clusters lower down on the same branches -

thus rendering the species unmistakably monoecious. The condition in *C. odorata* is obviously that of a monoecious species, though no sex change over time could be demonstrated. From these findings it can be deduced that those species that have traditionally been held to be dioecious, may have been wrongly labeled thus. Single observations of the plant can miss the phenomenon of morphological plasticity and its inherent sex change over time and give rise to this misconception.

Wind-pollination is generally seen as a common alternative to biotic pollination in species-poor or cool habitats where the survival of biotic pollinators would be difficult. Yet, wind-pollination has evolved in the species-rich and structurally dense Fynbos of the Cape Floral Kingdom, and is found in the Ericaceae, Proteaceae, Asteraceae (*Tarconanthus*) and Rosaceae (*Cliffortia*) (le Maitre & Midgley 1992). Accepted as a primitive condition in the gymnosperms, it had been confirmed in the Cape genera *Podocarpus* and *Widdringtonia* (Phillips 1926; Koutnik 1987). While sharing most of the adaptive characters (Proctor 1996; Koutnik 1987) with other wind-pollinated plants, the coniferous species of *Cliffortia* have a rare reversal of the location on the plant, of the male and female elements, with the male below the female. This rare condition is shared with only one evergreen gymnosperm, viz. *Pinus sylvestris* (see more below) (Proctor 1996).

Although only eight species of the 119 in *Cliffortia* were included in this study, they are representative of the types of inflorescences in the genus, covering the range from the single flowered inflorescence in *C. nivenioides,* to the highly condensed and discrete female cone in *C. conifera*. There are also similarities between each of the different types of inflorescences in this genus and those of various monoecious wind-pollinated genera with condensed inflorescences, like the heads or spikes of *Sanguisorba* (the closest relative of *Cliffortia* in the Rosaceae) (Nordborg 1966; Zohary 1972), the spikelets of the Poaceae, the catkin-like spikes of the Cyperaceae, the condensed umbels of the Juncaceae, and the catkins of the Betulaceae and Corylaceae. The most remarkable parallelism, however, is seen in the three coniferous species of *Cliffortia,* particularly the most highly evolved *C. conifera,* and the serotinous evergreen Gymnospermae. Not only are these conifers evergreen, serotinous and monoecious like the coniferous *Cliffortia* species, but in *Pinus sylvestris* the male strobili are borne lower down on the shoots which bear the female cones apically (Proctor et al. 1996), similarly to the condition in *C. arborea, C. dichotoma* and *C. conifera*. The question arises as to whether this condition could be an adaptation to pollination by up-drafts prevailing at the edges of the escarpments that are the preferred habitats of these species.

A phenomenon apparently peculiar to *Cliffortia* among the anemophilous plants and occurring in all but one of its species, is the morphological plasticity of the inflorescence, resulting from the retention of the viability of the apical buds of the short shoots forming the matrix of all inflorescences in the genus. This plasticity has a marked effect on the vegetative branching pattern as well as on the sexuality of the plant, facilitating a sex change over time.

In wind-pollinated plants with inflorescences similar to those of the various non-coniferous *Cliffortia* types, such as the grasses, sedges and rushes, the inflorescence shows none of this plasticity but is instead a highly specialized structure dedicated to the bearing of flowers, after which it is discarded without contributing to the vegetative increase or growth pattern of the plant. There is also no evidence of a sex change in these taxa. In *Cliffortia*, the only analogue for this degree of dedication with non-contribution to the subsequent vegetative development and thus the branching pattern, is found in the highly specialized female inflorescence of *C. conifera,* which is borne on a dedicated lateral branch. Here the inflorescence has no viable apical buds and thus no apical proliferation. It also lacks internodal elongation. It has lost the plasticity seen in varying degrees in the rest of the species. Sex change has also been excluded in all three the coniferous species.

In species with pronounced morphological plasticity and therefore, obvious sex changes, monoecy is readily acceptable. This is also the case with the coniferous species with unisexual inflorescences borne on the same plant. It is however, not so discernable in species with vegetative apical proliferation as the only morphological change to the basic or simple multi-flowered short shoot inflorescence. In these instances, careful monitoring of individual plants in situ can complement the observations of segregation of the sexes in time. This was demonstrated in the linear inflorescences or partial inflorescences in *C. ruscifolia, C. crenata* and *C. heterophylla*, with the female flowers appearing first. It was also the case in the clustered single-flowered inflorescences in *C. nivenioides* with the male flowers lower down in the cluster and therefore older.

Establishing monoecy in *Cliffortia* concurs with the finding of a strong association between wind-pollination and monoecy as recorded in a study in Britain (Proctor et al. 1996). Although only limited in number, the selection of the species for this study was not done on the basis of the distribution of male and female flowers, but for their variety in inflorescence morphology. Thus, finding all of these species to be monoecious, is in sharp contrast to the popular view that dioecy is the norm for the genus with about 60 % of species 'capable of being monoecious' as stated by Weimarck (1934). Past studies had been based on single observations of a specimen. As a result, the shift in predominance of male or female elements in an individual plant over time, has been overlooked. This shift becomes apparent only when an individual plant is carefully monitored over a whole season. The case of *C. heterophylla* with its obvious morphological metamorphosis accompanying the shift from the female to the male stage, is a prime example of the possible erroneous interpretation of these morphologically different stages as morphologically different plants, when based on a single observation of any one plant. In fact, *C. heterophylla* displays the shift excellently because of its relative size and the presence of leaf differentiation. The interpretation of the patently bi-sexual individuals as the inflorescence at the peak of development, and not as an anomaly, is crucial in deciding the sexuality of this species. In the light of the findings in this study, an earlier published description of *C. burgersii* (Oliver & Fellingham 1991) as being dioecious, might reflect yet another example of the possible erroneous interpretation of morphologically different stages of a monoecious plant, as morphologically different plants of a dioecious species.

The commonly held view that sex is genetically controlled (Wilson et al. 1978; Haney 1978; Fuller et al. 1972; Fuller and Ritchie 1967; Garber 1972; Burns 1969; Strickberger 1976; Grant 1975; Gardener 1975), has only rarely been challenged by the recognition that the sexual state of individuals can sometimes change (Yampolsky 1919; Heslop-Harrison 1924; Hartman 1956; Smith 1963). Sex changing (or sequential hermaphroditism) as 'a phenomenon of at least some dioecious species', has more recently been based on findings in 66 species in 25 families, documented from as early as 1910 (Freeman et al. 1980). 'Apparent dioecy' in any one season, masking the true labile nature of the sex of the plant which can change with changes in the physiological state, which in turn depends on external factors, was described in *Arisaema triphyllum* (Araceae) by Bierzychudek (1982). She also found that all *Arisaema* species change sex, though only some change from male to female without any hermaphrodites. Similar findings of sex changes were reported in *Myrica gale* (Myricaceae) (Proctor et al. 1996).

While the factors that control sex and sex changes in *Cliffortia* are not known at this juncture, the phenomenon of morphological plasticity and its roll in sex change, with the subsequent determination of the plant as monoecious, is clear.

Chapter 5: Conclusions

The short shoot:

In all of the species studied, flower-bearing was conclusively shown as the function of a short shoot, even in the case of the male flowers. The flower is borne laterally on the short shoot, and not apically, leaving the apical bud of the short shoot potentially viable. The leaf subtending the flower on the short shoot is modified to become a bract, or reduced, leaving the flower e-bracteate. In the latter instance, the flower is borne on a reduced short shoot which is the axis of a basic single-flowered inflorescence, borne in the axil of a vegetative leaf. In the past this basic single-flowered inflorescence had been interpreted as a single flower on its pedicel in the axil of a vegetative leaf. This caused the confusion as to the stance of the flower and the presence of a viable apical bud, occupying the same leaf axil as the flower.

The demonstration of the existence of a single-flowered inflorescence as the basic flower-bearing structure in the early developmental stage of the inflorescence in *C. heterophylla, C. crenata* and *C. odorata* - the latter two species having been declared by Weimarck as having 'no brachyblasts'-shed new light on the role of the short shoot in the fertile stage. Even the late proliferating single-flowered inflorescence in *C. nivenioides,* makes sense when interpreted as an inflorescence that is limited to the production of that single flower in the fertile stage, after which the apical bud remains dormant till the following vegetative stage, when it proliferates into a vegetative short shoot. (The predominance of short shoots in the vegetative structure of this species, is a peculiarity that can be linked to the fact that the only origin of long shoots is the lengthening of the rare fertile short shoots during the later stage of flowering.)

Concerning the role of the short shoot in flower-bearing, the following conclusions can be drawn:

Firstly, short shoots are always present in the fertile stage even if only as hardly visible, single-flowered, highly condensed inflorescences.

Secondly, no flowers are borne directly in the axils of ordinary vegetative leaves on long or short shoots. In fact, it is exactly when this appears to be the case, as in the above mentioned four species, that the highly condensed inflorescence occurs, bearing the flower(s) laterally in the axils of much reduced and modified bracts.

Thirdly, the basic flower-bearing structure, though always a short shoot, is not always a highly condensed inflorescence. It can be a visible short shoot with permanently short internodes as in *C. ruscifolia*, but then the subtending leaves are clearly modified bracts.

These conclusions hold for the male flowers as well, although in species where the male flowers develop on the proliferation shoot, further investigation is warranted. In species with an admix of the sexes in one inflorescence, there can be no question. In the female cone-bearing species, the male flowers occur in small, apparently e-bracteate fascicles and, by implication, in a primordial inflorescence.

Short shoots and long shoots:

The short shoot axis of an inflorescence can either lengthen to become a long shoot or proliferate apically into a vegetative shoot (usually a long shoot), or lengthen and proliferate. These changes can take place during the development of the inflorescence or at the onset of the vegetative stage, designating the majority of short shoots as functional in the flowering stage and long shoots in the vegetative.

The vegetative axes producing discreet inflorescences, are always long shoots. Discreet inflorescences are always borne in the axils of ordinary vegetative leaves on these long shoots.

Rare apparently fertile vegetative short shoots do occur as in *C. nivenioides* but undergo internodal lengthening to render them long shoots, thus revealing their true character as vegetative axes for the discreet inflorescences originating in the axils of their vegetative leaves.

Defining the inflorescence:

The most prevalent mode of flower-bearing in the genus is thus not that of ' solitary flowers in the axils of ordinary vegetative leaves' as Weimarck (1934) described it, but that of the single-flowered inflorescence with an e-bracteate flower on the single node of its condensed short shoot, with or without a viable apical bud. The basic inflorescence can thus be defined as a permanent or impermanent short shoot, consisting of one or more internodes, bearing a lateral flower or flowers, e-bracteate or in the axil(s) of a bract or bracts, the short shoot itself being borne in the axil of a vegetative leaf.

The acceptance of this definition firmly establishes the presence of the short shoot as an essential element of the flower-bearing structure in all species. Furthermore, it advances the understanding of the relationship between long shoots and short shoots and their involvement in determining the various branching patterns in *Cliffortia.*

Morphological plasticity and sex change:

Morphological plasticity of the inflorescence is caused by the changes in its short shoot axes. It can result in the total disappearance of the inflorescence through integration into the vegetative structure of the plant. When these changes take place during the development of the inflorescence, they facilitate a sex change as well as determine the vegetative branching pattern. Changes at the onset of the vegetative stage have an influence on the branching pattern only. Not all species exhibit a sex change but in all the species in this study, some influence of the inflorescence on the branching pattern was demonstrated.

The sex change facilitated by the morphological plasticity of the inflorescence, establishes the sexual status of the plant as monoecy. In the species not exhibiting plasticity during the development of the inflorescence and therefore not exhibiting a clear sex change, both sexes are present at the same time, thus rendering them indisputably monoecious, but in these the male and female flowers are never at the same stage of development at the same time. In cases where obvious sex changes take place, as well as those with both sexes present on the same plant or even in the same inflorescence, the sexes are thus separated in time, making the plant dichogamous. The condition in *Cliffortia* is thus monoecy with dichogamy.

Inflorescence type and branching pattern:

While there is an obvious link between the type of inflorescence and the branching pattern, it is strongly biased towards the monopodial, as in most species the apical bud of the main stem remains viable. This is true even in the case of the highly modified and condensed inflorescence of *C. arborea,* with the main axis of its primary short shoot also the main stem. In this species the linear growth of the main stem is only temporarily slowed down while the cone develops around it, to be resumed again as soon as the inflorescence has reached maturity. In older plants the pattern becomes obscured through the multiplicity of main branches, which in turn bear inflorescences. Only in *C. conifera* is there no direct influence of the inflorescence on the branching pattern except in the fact that the female inflorescences displace the normal vegetative branches in the fertile zone.

Sexuality of the plant:

All the species in this study are monoecious, though in some cases this only became clear after careful and repeated observations were made. It has been established that a plant can undergo different stages of development starting with an overtly male or female stage, changing to the opposite sex and alternating this brief fertile stage with the vegetative stage. A single observation of such a plant in either the overtly male or overtly female stage of development, can lead to the erroneous interpretation of the sexuality of the species. If interpreted as apparent dioecy with sequential hermaphroditism as in the case of *Arisaema* (Araceae) (Bierzychudek 1982), it would have to have a concise cut-off point of switching from one sex to the other. In *Cliffortia* elements of both sexes are present at the same time though never at the same stage of development. The male and female elements are thus separated in time, making the plant dichogamous.

Apparent dioecy with sequential hermaphroditism (or sex change) as described above, could be merely alternative terminology for monoecy with change over time in predominance of one or the other sex, thus constituting dichogamy, as illustrated in this study of *Cliffortia*.

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